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## Macrozooplankton and micronekton diversity and associated carbon vertical patterns and fluxes under distinct productive conditions around the Kerguelen Islands

Cédric Cotté, A. Ariza, Adrien Berne, J. Habasque, Anne Lebourges-Dhaussy, G. Roudaut, B. Espinasse, B.P.V. Hunt, E.A. Pakhomov, N. Henschke, et al.

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1       **Macrozooplankton and micronekton diversity and associated carbon**  
2       **vertical patterns and fluxes under distinct productive conditions around**  
3       **the Kerguelen Islands**

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32 **Abstract**

33

34 Mesopelagic communities are characterized by a large biomass of diverse macrozooplankton and  
35 micronekton (MM) performing diel vertical migration (DVM) connecting the surface to the deeper  
36 ocean and contributing to biogeochemical fluxes. In the Southern Ocean, a prominent High Nutrient  
37 Low Chlorophyll (HNLC) and low carbon export region, the contribution of MM to the vertical carbon  
38 flux of the biological pump remains largely unknown. Furthermore, few studies have investigated MM  
39 communities and vertical flux in naturally iron fertilized areas associated with shallow bathymetry. In  
40 this study, we assessed the MM community diversity, abundance and biomass in the Kerguelen Island  
41 region, including two stations in the HNLC region upstream of the islands, and two stations in naturally  
42 iron fertilized areas, one on the Plateau, and one downstream of the Plateau. The MM community was  
43 examined using a combination of trawl sampling and acoustic measurements at 18 and 38 kHz from the  
44 surface to 800m. A conspicuous three-layer vertical system was observed in all areas - a shallow  
45 scattering layer, SSL, between 10 and 200 m; mid-depth scattering layer, MSL, between 200 and 500  
46 m; deep scattering layer, DSL, between 500 and 800 m - but communities differing among stations.  
47 While salps (*Salpa thompsoni*) dominated the biomass at the productive Kerguelen Plateau and the  
48 downstream station, they were scarce in the HNLC upstream area. In addition, crustaceans (mainly  
49 *Euphausia vallentini* and *Themisto gaudichaudii*) were particularly abundant over the Plateau,  
50 representing a large, although varying, carbon stock in the 0-500 m water layer. Mesopelagic fish were  
51 prominent below 400m where they formed permanent or migrant layers accounting for the main source  
52 of carbon biomass. Through these spatial and temporal sources of variability, complex patterns of the  
53 MM vertical distribution and associated carbon content were identified. The total carbon flux mediated  
54 by migratory myctophids at the four stations was quantified. While this flux was likely underestimated,  
55 this study identified the main components and mechanisms of active carbon export in the region and  
56 how they are modulated by complex topography and land mass effects.

57

58

59 **Keywords:** macrozooplankton; micronekton; vertical patterns; active carbon flux; spatio-temporal  
60 variability; scattering layers; Kerguelen Plateau; Southern Ocean

## 61 **Introduction**

62 The mesopelagic community is composed of taxonomically and functionally diverse groups of  
63 organisms, including gelatinous organisms, crustaceans and mesopelagic fish, that occupy the 200-  
64 1000 m depth zone in the ocean. Through modelling and *in-situ* studies, mesopelagic organisms have  
65 gained increasing attention from the ecological and biogeochemical communities (Davison et al., 2013,  
66 Anderson et al., 2018, Hernández-León et al., 2019) and from managers interested in the sustainable  
67 exploitation of potential new resources (Grimaldo et al., 2020). This interest has primarily been  
68 stimulated by two characteristics of the mesopelagic zooplankton and micronekton. First, while  
69 logistical and technological difficulties in reliably estimating zooplankton and fish biomass still exist,  
70 recent assessments have pointed to a high likelihood of these populations being substantially  
71 underestimated (Irigoien et al., 2014, Hernández-León et al., 2020). Secondly, mesopelagic organisms  
72 are known to perform extensive diel vertical migration (DVM), described as the largest animal  
73 migration on Earth (Longhurst, 1976; Behrenfeld et al., 2019), between the mesopelagic zone (200-  
74 1000 m) during the day and the epipelagic zone (0-200 m) to feed at night.. This vertical movement  
75 connects the mesopelagic and epipelagic zones and represents an important active contribution in the  
76 downward flux of organic matter, and particularly the export of carbon to the deep ocean (Bianchi et  
77 al., 2013; Ariza et al., 2015).

78  
79 The Southern Ocean is the world ocean's largest high nutrient low chlorophyll (HNLC) area where the  
80 primary production is mainly limited by iron (de Baar et al., 1995). Naturally iron-fertilized sites  
81 generate highly productive regions in the Southern Ocean (Blain et al., 2007). The Kerguelen Plateau  
82 forms a large physical barrier to the eastward flowing Antarctic Circumpolar Current (ACC) and  
83 induces iron enrichment of shelf waters that are entrained in the downstream area eastward of the  
84 Plateau (Blain et al., 2007, Mongin et al., 2008). While upstream waters approaching the Kerguelen  
85 Islands are generally depleted in iron and chlorophyll (Jandel et al., 1998), a large bloom occurs over  
86 the Kerguelen Plateau as well as in the downstream region, observed as temporally persistent (over the  
87 spring and early summer period) and spatially dynamic high-chlorophyll plume (d'Ovidio et al., 2015).  
88 While these productive areas contribute to the sink of atmospheric CO<sub>2</sub> through photosynthesis , an  
89 inverse relationship has been observed between production and particulate carbon flux in the Kerguelen  
90 area (Savoie et al., 2008), which has also been observed elsewhere in the Southern Ocean (Maiti et al.,  
91 2013, Le Moigne et al., 2016). However, to date research has focussed on passive carbon flux in this  
92 region, and the contribution of active carbon flux remains unresolved. Given the prominent role of the

93 Southern Ocean in the global carbon cycle, active carbon flux needs to be addressed to assess the  
94 contribution of the active migrating community of organisms. This community includes a large variety  
95 of macrozooplankton and micronekton (MM) performing DVMs of variable magnitudes (e.g., Roe et  
96 al., 1984). The knowledge gap of their role in ecosystems, including the diversity and contribution in  
97 biogeochemical stocks and flux, has recently been stressed (Ratnarajah et al., 2020, Martin et al.,  
98 2020).

99

100 The Kerguelen area (i.e., the Plateau and surrounding upstream and downstream waters) offers ideal  
101 conditions to investigate the diversity of pelagic ecosystems and the associated active biological pump  
102 at a site of natural iron fertilization and contrasting production regimes. This region is also ecologically  
103 important as a foraging ground for several species of land-based marine top predators often used as  
104 bioindicators of productive areas and rich trophic webs (Hindell et al., 2011). Their diet is largely  
105 comprised of MM and the estimated food consumption by the highest trophic level predators indicates  
106 the presence of significant standing stock of mesopelagic micronekton, primarily myctophids, and  
107 macrozooplankton, including euphausiids and hyperiids (Guinet et al., 1996, Bocher et al., 2001, Bost  
108 et al., 2002, Cherel et al., 2002, Lea et al., 2002, Cherel et al., 2008). In this subantarctic area of the  
109 Southern Ocean, high abundances of intermediate trophic levels have been reported in association with  
110 either circumpolar frontal regions or local bathymetry-driven features (Pakhomov et al., 1994,  
111 Pakhomov and Froneman 1999, Behagle et al., 2017). For instance, the abundance of the subantarctic  
112 krill *Euphausia vallentini* was associated with the shelf topography and the location of the Polar Front,  
113 and it was reported to be more numerous in the eastern area than in the western part of the Kerguelen  
114 region (Koubbi et al., 2011, Hunt et al., 2011). It has recently been reported that, on a global scale,  
115 zooplankton biomass in the whole water column increases with the average net primary production,  
116 implying an enhanced active flux of carbon coupling the surface and deep layers (Hernández-León et  
117 al., 2020).

118

119 The main objective of this study was to understand how mid-trophic level MM respond to contrasting  
120 production regimes (oligotrophic vs biologically-enriched zones) in the Kerguelen area. Specifically,  
121 we investigated the patterns and the variability of MM using a combination of stratified midwater trawl  
122 sampling and acoustic measurements. First, we tested the hypothesis that high primary production  
123 implied high abundance of MM as reported in other areas (Irigoiien et al., 2014, Hernández-León et al.,  
124 2020). This response in terms of communities and densities was analysed within the Kerguelen  
125 seascape, describing the MM spatial variability. Second, the vertical pattern of variability was

126 examined and particularly how the vertical distribution of the various taxonomic groups differed  
127 between night and day according to the previously described communities. This knowledge on MM  
128 abundance and diel cycles according to the production and oceanographic seascape is fundamental to  
129 estimate the contribution of these organisms to the energy transfer along the food web. Finally, we  
130 assessed the vertical distribution of energy through the depth-stratified carbon content of the different  
131 taxonomic groups. Additionally, we estimated carbon flux mediated by myctophids based on family-  
132 specific physiological rates (Pakhomov et al., 1996; Belcher et al., 2019). While it was expected that  
133 productive areas also implied abundant mesopelagic fish (Irigoiien et al., 2014), the contribution of  
134 these active migrators in vertical flux was assessed in HNLC *vs* productive area.

## 135 **Methods**

### 136 **- Survey**

137 The Mobydick survey (DOI: <https://doi.org/10.17600/18000403>) was carried out south of the  
138 Kerguelen Islands onboard the *R/V Marion Dufresne II*. From the 26th of February to the 19th of  
139 March 2018, hydrographic and acoustic data, as well as MM samples were collected at four stations  
140 (M1, M2, M3 and M4, Fig. 1). The comparative approach used in this study, targeting iron fertilized vs  
141 HNLC sites, originated from the scientific strategy of the KEOPS 1 and 2 campaigns (Queguiner et al.,  
142 2011). These stations were located based on knowledge from previous oceanographic cruises  
143 conducted in the area (e.g., Blain et al., 2007, d'Ovidio et al., 2015, Behagle et al., 2017). The M1  
144 station was located east of the Plateau, downstream of the ACC, in the spring bloom areas known as the  
145 Kerguelen plume (d'Ovidio et al. 2015), also identified as the core foraging area of the king penguin, an  
146 important top predator in terms of consuming biomass (Scheffer et al., 2016). The M2 station located  
147 on the Plateau (isobath 520 m) corresponded to a reference station to study the naturally fertilised  
148 spring bloom on the Kerguelen Plateau (Quéguiner et al. 2011). West of the Plateau, the upstream  
149 stations M3 and M4 were chosen because HNLC conditions prevailed. While M1 was visited once, M4  
150 was visited twice and M2 thrice. The first visit of the M3 station with a full sampling of all depths  
151 during daytime and nighttime was divided into two periods because of bad weather conditions, so that  
152 M3-1 and M3-2 were separated by 11 days.

153

### 154 **- Remote and in-situ oceanographic measurements**

155 Hydrological casts were carried out at each visit of all stations (Fig. 1). Temperature (T) and  
156 chlorophyll *a* concentration (Chl *a*) profiles were collected using a SeaBird SBE 19+ Conductivity-  
157 Temperature-Depth (CTD) probe equipped with a calibrated Chelsea Aqua-Tracker Mk3 fluorometer  
158 mounted to a rosette frame holding Niskin bottles. The rosette was hauled at a speed of 1 m.s<sup>-1</sup> between  
159 Niskin samples. Water collected in the Niskin bottles was used for chlorophyll *a* extraction and HPLC  
160 analysis as per Uitz et al. (2008). Conversion from the fluorometer measurements to Chl *a* was  
161 performed by estimating a linear fit between CTD fluorometer readings and corresponding Niskin  
162 bottle samples ( $n = 40$ ,  $R^2 = 0.93$ ). The mixed layer depth (MLD) was determined from the minimum  
163 depth to which  $T < T_{10m} - 0.4$  °C (Condie and Dunn, 2006).

164

165 Sea surface chlorophyll data from Global Ocean Color products with a 1/24° resolution (product id:  
166 OCEANCOLOUR\_GLO\_CHL\_L4\_REP\_OBSERVATIONS\_009\_082 from the Marine Copernicus

167 data portal: <https://www.copernicus.eu>) produced by ACRI-ST was used to build time series of Chl *a* at  
168 each station. We considered the weekly averaged L4-product (7 days) of merged satellite observations  
169 to describe the bloom temporal patterns since it represents a good compromise between the temporal  
170 resolution and the cloud coverage. We also estimated the Polar Front (PF) mean location in the  
171 Kerguelen area by using T and S profiles from the Global Ocean Reanalysis (Ferry et al., 2016), as  
172 described in Pauthenet et al. (2018).

173

#### 174 - **Acoustic measurements**

175 Continuous acoustic measurements were made with a calibrated (Demer et al., 2015, Simrad EK80  
176 documentation) Simrad EK80 echosounder operating at five frequencies: 18, 38, 70, 120 and 200 kHz.  
177 As we were interested in describing acoustic scattering in epipelagic and mesopelagic waters, we only  
178 used the 18 and 38 kHz frequencies, with maximum acquisition ranges of 1000 and 800 m respectively.  
179 Power and pulse length were respectively 2000 W and 1024  $\mu$ s for 18 kHz and 1000 W and 2048  $\mu$ s for  
180 38 kHz. Data used in this study were acquired with an average ping interval of 3 s, mostly during  
181 station time when the vessel was either immobile or during trawling activity.

182 The acoustic data were scrutinized, corrected and analysed using the “Movies3D” software developed  
183 at the “Institut Français de Recherche pour l'Exploitation de la Mer” (Ifremer; Trenkel et al., 2009)  
184 combined with the French “Institut de Recherche pour le Développement” (IRD) open-source tool  
185 “Matecho” (Perrot et al., 2018), developed in MATLAB. The noise from the surface were removed  
186 (from 3 m below the transducer, i.e., surface 12 m removed) and the bottom ghost echoes were  
187 excluded and the bottom line was corrected. Single-ping interferences from electrical noise or other  
188 acoustic instruments (Le Bouffant, N., *comm. pers.*), and periods with either noise or attenuated signal  
189 due to inclement weather, were removed using the filters described by Ryan et al. (2015). Background  
190 noise was estimated and subtracted using methods described by De Robertis and Higginbottom (2007).  
191 The nautical area scattering coefficient (NASC in  $\text{m}^2 \text{nmi}^{-2}$ ), an indicator of marine organisms'  
192 biomass, and the volume backscattering strength (Sv in  $\text{dB re } 1\text{m}^{-1}$ ), an indicator of the marine  
193 organisms' density, were calculated. Acoustic symbols and units used here follow MacLennan et al.  
194 (2002). Data were echo-integrated into 0.5 m high layers over a 3 pings period giving one ESU  
195 (Elementary Sampling Unit) with a -100 dB threshold from 12 m down to 800 m depth.

196

197 DVM is a common behaviour for zooplankton and micronekton that can be observed at almost all  
198 spatial scales (Haury et al., 1978). Acoustic data were thus split into day, night and crepuscular periods



199 (dawn and dusk). Day and night periods were defined based on the solar elevation angle with day when  
200 sun elevation is  $>18^\circ$  and night with sun elevation  $<-18^\circ$  (as in Lehodey et al., 2014).  
201 Acoustic data were also spatially split between stations by creating a  $0.8^\circ$  Longitude by  $0.5^\circ$  Latitude  
202 rectangle around the GPS coordinate of each station (Fig. 1, blue rectangles). These rectangular areas at  
203 each station encompass the trawl operations area. Acoustic data recorded during transits (i.e., out of  
204 these spatial limits) were excluded from data analysis. The vertical profiles of mean acoustic density  
205 NASC were computed for each visit of each station for the daytime and nighttime periods (not only  
206 trawling time).

207

208 *Data visualisation*- Red Green Blue (RGB) composite images were generated in MATLAB based on  
209 the 18 and 38 kHz echo-integrated acoustic data as in Annasawmy et al. (2019). The acoustic volume  
210 backscattering strength Sv of the 18 kHz frequency was colour-coded in red while the 38 kHz was  
211 displayed in colder hue using both blue and green, with a high threshold scale of -60 dB and a low  
212 scale threshold of -90 dB. In the RGB composite image subsequently created, the hue gives the  
213 frequency with the highest backscatter and the luminance gives the intensity of the volume  
214 backscattering strength. A light cyan (combination of blue and green) colour indicates a dominant and  
215 high 38 kHz backscatter whereas a dark red colour indicates a dominant but low 18 kHz backscatter. A  
216 black hue indicates that all backscatters are under the low scale threshold or that no data are available,  
217 and a white hue indicates that all backscatters are above the high threshold scale. Using these two  
218 frequencies, the RGB echogram gave for each station, a clear and synthetic visual representation of the  
219 location and migration in the water column of acoustic communities of scatterers based on their most  
220 resonant frequency from 20 to 800 m.

221

## 222 - **Trawling**

223 Forty-eight trawls were performed, consisting of three nighttime trawls and three daytime trawls at  
224 each station (Table 1). MM were collected during daytime and nighttime using a Mesopelagos trawl,  
225 designed by Ifremer (fisheries biology and technology laboratory, LTBH, Lorient, France) (Meillat,  
226 2012). This non-closing trawl has a 7 m mean vertical opening and 12 m horizontal opening, with a 65  
227 m<sup>2</sup> mouth area and 44 m length. The trawl has a mesh size of 30 mm in the wings, reducing to 4 mm in  
228 the codend, so that it was used to target organisms ranging in size from approximately 1–30 cm long.  
229 Trawl depth was monitored in real-time with a Scanmar (Åsgårdstrand, Norway) depth sensor attached  
230 to the trawl headline. We adopted a semi-stratified/adaptive strategy in trawl sampling. As one aim of  
231 the study was to provide a detailed description of the micronekton community at each station, the

232 whole water column from the surface to 650 m was sampled at different strata corresponding to the  
233 sound scattering layers at different depths: the shallow scattering layers (SSL, between 10 and 200 m),  
234 the mid-depth scattering layers (MSL, between 200 and 500 m) and the deep scattering layers (DSL,  
235 between 500 and 800 m). At each layer, hauls were performed at targeted depths according to the  
236 observations of the different scattering structures (patches or layers) provided by the echosounders. The  
237 towing speed was maintained near 2 knots, with effective fishing times of 30 minutes. Our samples  
238 may consistently underestimate individuals smaller than the mesh size (30 mm), even slightly larger  
239 (40 mm) for micronekton with soft body such as salps. Selectivity of the mesopelagos is a shortcoming,  
240 particularly for species such as salps which can be sampled as individuals or aggregated chains. While  
241 underestimation of small individuals' may have occurred, this was consistent across all trawl  
242 deployments, i.e. across regions (Henschke et al. 2020).

243

244 Once on board, the total wet mass (WM) in grams was weighed. Organisms were first sorted into broad  
245 taxonomic groups (fish, crustaceans, gelatinous organisms and cephalopods), then identified at the  
246 species level. All organisms were counted and weighed and fish size was also measured using standard  
247 length (SL). The allocated temperature estimate for each trawl was performed by using the temperature  
248 profile from the CTD cast closest to the trawl location in space and time, and by taking the estimated  
249 temperature at the trawl depth (during the fishing period).

250

#### 251 - **Estimates of C content**

252 Carbon biomass was estimated using conversion factors to convert WM to dry mass (DM) and DM to  
253 carbon biomass for the four main taxonomic groups - gelatinous organisms, fish, molluscs and  
254 crustaceans. Water content for each of the groups was estimated based on available data from the  
255 literature: 94% for gelatinous organisms (Larson 1986, Huntley et al 1989), 75% and 80% for fish and  
256 molluscs, respectively, (Schaafsma et al., 2018) and 75% for crustaceans (Schaafsma et al., 2018,  
257 Harris et al., 2000). The carbon content of dry biomass was provided in the context of stable isotopes  
258 analysis (Hunt et al., this issue) carried out on all the main taxa. The percentage of C in DM was then  
259 averaged for each group such as gelatinous organisms 15%, fish 50%, molluscs 35% and crustaceans  
260 40%.

261

#### 262 - **Migrant biomass and carbon flux**

263 Additionally, biomass and carbon flux were estimated for migratory fish of the family Myctophidae.  
264 This group was selected among others, because it exhibited a clear diel vertical migration pattern, as

265 described previously in this area (Duhamel et al., 2000; Behagle et al., 2017) and detected in this study  
266 through the combined trawl and acoustic data. Additionally, family-specific metabolic equations were  
267 available to predict carbon fluxes in this group (Belcher et al., 2019). On the other hand, estimations in  
268 other migratory groups were unfeasible due to sampling limitations. For example, individual body  
269 length and mass, needed for the estimation of metabolism, could not be accurately and systematically  
270 measured in salps and euphausiids, due to the deterioration of samples during trawling. We assumed  
271 that all myctophids found at nighttime in the SSL would return to MSL or DSL during daytime.  
272 Migration was then calculated as the abundance and biomass of myctophids in the nocturnal shallow  
273 trawls (ID) 5, 6, 11, 19, 20, 21, 31, 35, 37, 39, and 48 (Table 1). This was standardized for the volume  
274 filtered by the net, and it was integrated by the thickness of the sound scattering layer (from  
275 echograms) where the net was located. Abundance and biomass were expressed as the number of  
276 individuals or the milligrams of carbon weight per square metre ( $\text{ind m}^{-2}$ ,  $\text{mg C m}^{-2}$ ).

277

278 Carbon flux mediated by respiration was estimated by calculating the amount of carbon dioxide  
279 exhaled by myctophids below the maximum MLD in the region, which was 120 m depth. The  
280 respiration rate for each individual was estimated using body mass and environmental temperature as  
281 predictors, following the respiration regression developed for myctophid fish in Belcher et al. (2019):

282

$$283 \quad \text{Ln}(R_{WM}) = -1.315 - 0.2665 \times \text{Ln}(WM) + 0.0848 \times T \quad \text{Eq. 1}$$

284

285 where  $R_{WM}$  is the mass-specific respiration rate per hour ( $\mu\text{l O}_2 \text{ mg WM}^{-1} \text{ h}^{-1}$ ),  $WM$  is the individual  
286 wet mass (mg), and  $T$  is the environmental temperature ( $^{\circ}\text{C}$ ). Individual wet mass was estimated using  
287 the length-weight relationships provided for the family Myctophidae by Kwong et al. (2020).

288 Respiration was computed for  $2.2^{\circ}\text{C}$ , corresponding to the average temperature in waters between 400  
289 and 500 m depth. This interval was assumed as the end of migration, according to the daytime migrant  
290 layer depth registered with the echosounder. The total respiration for each trawl was calculated by  
291 standardising the volume filtered by the net (considering a cylinder with the mouth opening of the trawl  
292 opening and the distance travelled during the haul), and summing for all myctophid individuals caught  
293 in that trawl. Similar to the abundance and biomass measurements, total respiration was integrated by  
294 the thickness of the sound scattering layer that the net sampled. This was then converted to units of  
295 carbon per square meter and day ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ) using a respiratory quotient of 0.90 for fishes (Brett  
296 and Groves, 1979, Ariza et al., 2015) and the stoichiometric relationship between carbon and oxygen

297 (22.4 L O<sub>2</sub> = 12 g carbon). Since carbon flux to the mesopelagic zone only occurs during the daytime,  
298 only 12 hours were considered for calculations.

299

300 Carbon flux mediated by the egestion of faecal pellets, known as “gut flux”, was estimated assuming  
301 that myctophids fed to satiation at the surface before migrating down to the mesopelagic zone or  
302 deeper. The food ball weight was assumed to be 2.2% of the body carbon weight, considering the  
303 average maximum stomach fullness found for southern-ocean myctophid species by Pakhomov et al.  
304 (1996). Then we assumed a 15% of loss as faeces, following conservative estimations for midwater fish  
305 from Hopkins and Baird (1977). This egestion was assumed to be constant throughout the day, so it was  
306 divided by 24 hours to compute the hourly egestion. This was multiplied by the residence time at depth  
307 (12 hours) minus the gut passage time (5.6 hours) to calculate the total carbon exported through  
308 egestion in the MSL and DSL. Gut passage time was averaged from measurements compiled for  
309 myctophid species in Pakhomov et al. (1996). Excretion of dissolved organic carbon was not computed  
310 due to the lack of knowledge about this metabolic rate in midwater fishes (Hudson et al., 2014). The  
311 amount of carbon through this mechanism is however expected to be small as dissolved matter  
312 represents a negligible part of carnivorous fish egestion, being mainly composed by non-carbon  
313 compounds such as urea and ammonia (Brett and Groves, 1979).

314

315 Carbon flux mediated by mortality at depth was estimated assuming that this was equivalent to growth,  
316 considering that the system is in a steady-state (Hernández-León et al., 2019). Growth was assumed to  
317 be 66% of respiration using metabolic budgets for carnivorous fish (Brett and Groves, 1979). Similar,  
318 to respiration and gut flux, mortality was considered only for the 12 hours residence time at depth. It is  
319 assumed that the fate of carbon transferred via predation to higher trophic levels stays in the  
320 mesopelagic zone.

## 321 **Results**

### 322 **- Environmental conditions around the Kerguelen Plateau**

323 In addition to their location relative to the Plateau (on the Plateau vs upstream/downstream areas), the  
324 stations were also situated within the area of a particular oceanographic feature, the PF, which crossed  
325 the Plateau just south of the Kerguelen Islands (Fig. 1). The M1, M2 and M4 stations were located  
326 south of the PF, with varying distances to the PF mean location, while the M3 station was located north  
327 of this front (see also Henschke et al. 2020). During the cruise, the concentration of Chl *a* was higher at  
328 station M2 on the Plateau compared to the downstream and upstream stations (Fig. 2). Overall, the Chl  
329 *a* concentrations (both over and outside the Plateau) during the survey were considered low (<0.4 mg  
330 m<sup>-3</sup>) compared to the concentrations observed during the spring/summer period from October to  
331 January. Throughout this period, the highest Chl *a* was measured on the Plateau in mid-January.  
332 Medium values occurred upstream (M3 and M4) with a simultaneous peak. An earlier (late November)  
333 maximum was observed downstream.

334

### 335 **- Description of the macrozooplankton/micronekton community from trawl collection.**

336 Over the whole study area, the dominant biomass from obtained from the trawl samples was attributed  
337 to gelatinous organisms (Fig. 3). In most trawls, they constituted a major part of the absolute biomass,  
338 i.e. an average wet weight per sample of 3497 g ( $\pm 7837$  g) corresponding to a mean proportion of 63 %  
339 ( $\pm 33.35$  %) of the total weight (supplemental material 1). This was followed by crustaceans, with an  
340 average weight per sample of 312 g ( $\pm 275$  g) corresponding to a mean proportion of 30 % ( $\pm 31$  %), and  
341 fish with an average weight per sample of 133 g ( $\pm 193$  g) corresponding to a mean proportion of 6.5 %  
342 ( $\pm 10.4$  %).

343 In trawls with a low total biomass (<1000 g), crustaceans had a higher relative biomass (supplemental  
344 material 1), particularly for samples carried out during daytime at depths shallower than 300 m. This  
345 trend was supported by the high relative abundance of crustaceans, which contributed more than half of  
346 the total organisms in 75 % of the 48 trawls (supplemental material 2).

347

348 In terms of biomass, the most important gelatinous contributors were salps (*Salpa thompsoni*) followed  
349 by siphonophores (especially *Rosacea plicata*) (Fig. 4 and Table 2). Notably, *S. thompsoni* was only  
350 abundant at stations M1 and M2. Chaetognaths were also often found in trawls with relatively low  
351 biomass. Ctenophores (*Bolinopsis* sp.) and jellyfish (mostly scyphozoans) had variable contribution to  
352 the proportion of gelatinous organisms with species occurring in half of the trawls (e.g., *Calyropsis*

353 *borchgrevinki*) and contributing weakly to moderately to biomass (such as *Atolla wyvillei* and  
354 *Periphylla periphylla*).

355

356 For crustaceans, the most common species in terms of occurrence and abundance were the euphausiid  
357 *E. vallentini* and the hyperiid amphipod *Themisto gaudichaudii* (Fig. 5 and Table 3). The latter was the  
358 only species among all taxonomic groups found in all trawls, but it was particularly abundant at M2  
359 over the shelf. The euphausiid *Euphausia triacantha* was also frequently found, though with a lower  
360 abundance than *E. vallentini*. Other hyperiid amphipods, e.g. *Cyllopus magellanicus* and *Primno*  
361 *macropa*, often occurred in trawls albeit at relatively low abundances.

362

363 The dominant fish family was myctophid with 3367 individuals belonging to 14 species (Fig. 6 for  
364 myctophids only, Table 4 and supplemental material 1 for the main fish species). The most abundant  
365 species within the whole fish community was *Krefflichthys anderssoni*, which represents half of the  
366 fish caught when merging adults and post-larvae. *Electrona antarctica* was also an abundant species  
367 and the most frequent fish in all trawls. Other myctophids, such as *Gymnoscopelus braueri* and  
368 *Protomyctophum bolini* had a high occurrence but were low to moderately abundant. Other fish  
369 families were characterized by either a high occurrence (i.e., *Notolepis coatsi* for Paralepididae) or  
370 locally a high abundance (e.g., *Bathylagus tenuis* for Bathylagidae, *Cyclothone* sp. for  
371 Gonostomatidae).

372

### 373 - Variability in vertical patterns from acoustic and trawl records

374 -Diel variability-

375 **Diel variability in biomass and acoustic densities:** A strong variability was observed in the vertical  
376 distribution of both biomass and acoustic densities between nighttime and daytime. Very low biomass  
377 was sampled in the SSL during daytime (Fig. 3). However, acoustic profiles indicated that high  
378 densities, organized in relatively thin peaks, occurred in this layer at ~100 m depth during both  
379 nighttime and daytime (Fig. 7). At depth, diel differences in biomass were less clear and acoustic  
380 densities were variable. Recurrent medium densities were observed between 400-500 m during daytime  
381 and between 250-400 m during nighttime. The 38 kHz backscatter was globally lower than the 18kHz  
382 between the surface and 500 m, while an opposite pattern occurred at depths >500 m. Although we  
383 observed (RGB echograms) diel vertical movements of acoustic structures and a patchy distribution of  
384 MM during daytime, a conspicuous 3-layers system characterized the whole area (Fig. 8). During  
385 daytime, clear scattering layers appeared and various patches, in terms of size and density, were

386 observed whereas acoustic layers were more scattered and consistent in the horizontal axis during  
387 nighttime. Transition periods (dusk and dawn) evidenced different patterns of vertical migrations  
388 between the surface and the underlying deeper layers, including vertical movements deeper than 800 m.  
389 Migratory organisms were more responsive at 18kHz, while a permanent non-migratory layer was  
390 observed at 600 m, which was characterized by an intense 38kHz signal (in dB).

391

392 **Diel variability in communities:** The most important diel variability in communities and relative  
393 biomass/abundance was observed in the SSL (i.e., above 200 m) (Fig. 3, 4, 5). The gelatinous MM  
394 (mainly salps) dominated biomass at nighttime at M1 and M2 and abundance at M1. During the night  
395 at M2, gelatinous groups and crustaceans had a similar abundance in the top 200 m layer. Crustaceans  
396 (mainly euphausiids at M1, M3 and M4 at night, Fig. 5) were lower in biomass but more abundant than  
397 gelatinous organisms. Myctophids (mainly *E. antarctica*, Fig. 6) were only present in this surface layer  
398 during nighttime. Between 200 and 500 m, gelatinous MM (mostly salps), contributed the most to total  
399 MM biomass during nighttime and a mixture with other gelatinous during daytime at M1 and M2,  
400 while siphonophores dominates the biomass in this layer at M3 and M4 (Fig. 4). Crustaceans (mainly  
401 euphausiids and hyperiids, Fig. 5) were also proportionally abundant during both periods of the day  
402 (supplemental material 2), while numerous at this depth only at M2 (Fig. 5). Fish mainly occurred in  
403 this MSL during nighttime (Fig. 6). Below 500 m (excluding the station M2), the biomass was similar  
404 for the three main taxonomic groups, in terms of both biomass and abundance, with a higher  
405 contribution of fish than in the upper layers (supplemental material 1, 2). This corresponded with  
406 higher myctophid abundance and also more bathylagids and cyclothones (supplemental material 1).  
407 Similar (relative) biomass and abundance were observed during nighttime and daytime within this  
408 DSL. Gelatinous organisms were similar to the MSL previously described, with an increased  
409 proportion of jellyfish occurring during nighttime (Fig. 4). Crustaceans presented similar biomass  
410 between nighttime and daytime.

411

412 *-Inter-station variability-* Lower biomass was reported for M3 and M4 stations during the nighttime in  
413 the (sub-)surface (shallower than 200 m). This main difference was mostly attributed to gelatinous  
414 organisms. While salps were abundant at M1 and M2 stations, they represented a low percentage of the  
415 gelatinous community at M3 and M4 (Table 2 and Fig. 4). The biomass at these latter stations was  
416 consequently considerably lower with a higher contribution of the other taxa, particularly  
417 siphonophores (occurring only deeper than 300m, including at M2) and to a lesser extent, ctenophores  
418 and jellyfish. Crustacean abundances between stations exhibited a different pattern. They were

419 numerous at the M2 station with a large proportion of the hyperiid *T. gaudichaudii* (Table 3 and Fig. 5).  
420 At other stations, euphausiids dominated the crustacean community, especially in surface waters during  
421 nighttime where large quantities were collected (at stations M1 and M4). Conversely to the crustacean  
422 pattern, the lowest abundances of fish, including the dominant myctophids, were found at M2. Despite  
423 low fish biomass at this station, a high diversity was found and *E. antarctica* was the most abundant  
424 species at all depths. At other stations, *K. anderssoni* was the dominant species, particularly in mid-  
425 depth and deeper waters during nighttime. However, *E. antarctica* was the most common species found  
426 in surface waters during nighttime and at depth during daytime. Finally, the main contrast observed in  
427 acoustic densities was reported between M2 and the other stations (Fig. 7).

428

429 *-Intra-station variability-* For stations visited twice (M4) or three times (M2 and M3), patterns of  
430 vertical distributions were consistent between visits, though some variability was observed. The  
431 variability was mostly observed in terms of biomass and abundance at similar depths, while the  
432 composition of the MM community was similar between visits. Acoustic profiles indicated some  
433 changes observed between visits. Densities observed during daytime at M2 decreased between the first  
434 (highest daytime biomass, Fig. 3) and the second visit. At M3 and M4, a global deepening of densities  
435 from MSL to DSL (highest fish biomass reported during the 2<sup>nd</sup> visit of M3) as well as an increase in  
436 the surface layer occurred between the first and the second visit, especially during nighttime.

437

#### 438 **- Carbon content in each taxonomic group**

439 Due to low carbon content, the contribution of gelatinous plankton to total carbon biomass was  
440 important but decreased significantly in comparison with their contribution to wet biomass (average of  
441 29.85 % ( $\pm 25.46$  %) for gelatinous, 51.69 % ( $\pm 31.04$  %) for crustaceans and 18.88 % ( $\pm 23.51$  %) for  
442 fish, Fig. 9). At most of the stations (M1, M3 and M4), fish dominated carbon biomass in the DSL  
443 (average of 38.37 % ( $\pm 26.37$  %)), especially for the night trawls (average of 50.54 % ( $\pm 22.49$  %)). In  
444 surface layers, crustaceans were usually the major contributors to carbon biomass, except for a few  
445 stations where gelatinous organisms were dominant (Fig. 9).

446

#### 447 **- Carbon flux**

448 The abundance, biomass, and carbon flux from myctophids entering the MSL and the DSL during  
449 daytime ranged from 0.001 to 0.163 ind m<sup>-2</sup>, from 0.04 to 15.08 mg C m<sup>-2</sup>, and from 0.001 to 0.091 mg  
450 C m<sup>-2</sup> d<sup>-1</sup>, respectively. According to Fig. 10, the downstream and upstream stations off the Plateau  
451 (respectively M1 and M4), exhibited the highest values of abundance, biomass, and carbon export,



452 while stations over and close to the Plateau (respectively M2 and M3) had the lowest values. Averaged  
453 Chl *a*, from 20 to 100 m depth, ranged from 0.19 to 0.60 mg m<sup>-3</sup> during the visits where carbon fluxes  
454 were estimated (Fig. 10a-b). As a result of the varying hydrographic conditions (MLD for instance)  
455 found at each visit, the distribution of migratory scattering layers changed as observed on echograms,  
456 and the depth range of trawling was adjusted to target these layers (e-h). The highest values on  
457 abundance, biomass, and carbon flux coincided with intermediate Chl *a* values in M1 and M4, in  
458 migratory layers sampled between 21 and 96 m depth (trawls 11, 21, 31 in Fig. 10), while the lowest  
459 values coincided with the Chl *a* maxima at M2, in migratory layers sampled between 21 and 175 m  
460 (trawls 37, 39 in Fig. 10). Carbon flux was fundamentally driven by biomass, which was in turn driven  
461 by the total number of individuals in the catch. This resulted from the overall similar size distributions  
462 between trawls, with individuals mostly ranging from 10 to 70 mm standard length (see supplementary  
463 material 2). Exceptionally, in trawls 6 and 20 at station M2, the occurrence of a few individuals larger  
464 than 100 mm increased the total biomass but decreased carbon flux as a result of lower metabolic rates  
465 of large fish (see equation 1). It is worthy to note that these two trawls were carried out in the SSL, but  
466 below the MLD.

## 467 **Discussion**

468 The waters surrounding the Kerguelen Islands encompassed variable communities of  
469 macrozooplankton-micronekton (MM), with respect to their biomasses, proportional contributions, and  
470 vertical patterns. Because vertical active fluxes are generally driven by biomass and composition, this  
471 has important implications for the regional and global biological pump (Ariza et al., 2015, Gorgues et  
472 al., 2019, Hernández-León et al., 2019). This study revealed the MM variability in response to the  
473 particular physical features and biological characteristics of this dynamic area.

474

### 475 **1. Macrozooplankton-micronekton communities within the Kerguelen seascape**

476 Our results provide a detailed description of the MM communities following a longitudinal gradient  
477 across the Kerguelen Plateau, and serves as a case study of an area of the Southern Ocean where  
478 contrasting production regions occur. As expected, the MM communities varied according to these  
479 environments differing in terms of bathymetry, downstream vs upstream location relative to the  
480 Plateau, level of Chl *a* and position relative to the PF (north vs south)

481

482 Over the Plateau area and south of the PF (M2), the MM community was rich in terms of abundance  
483 and biomass, especially for salps and crustaceans (*T. gaudichaudii*, as previously reported by Carlotti et  
484 al.(2015), and to a lower extent *E. vallentini*). Fish were less abundant but species diversity is higher  
485 compared to the other areas. While Chl *a* was relatively low during the sampling period, it had been  
486 preceded by a strong bloom. Indeed, this area is characterized by a reoccurring large phytoplankton  
487 bloom induced by naturally iron-fertilized waters from the Plateau (Blain et al., 2007). Sustained  
488 blooms as observed on the Plateau station favour a high secondary production rate and a general  
489 increase in zooplankton herbivory, as observed during the KEOPS2 survey (Carlotti et al., 2015). Low  
490 advection and high residence time occurring over the Plateau also support the hypothesis of local  
491 transfer of biomass through the trophic web (Henschke et al. 2015).

492

493 In the downstream area corresponding to the Kerguelen plume south of the PF (M1), salps largely  
494 dominated the biomass. Euphausiids (mainly *E. vallentini*) and fish (*K. anderssoni* and *E. antarctica*)  
495 were abundant in different layers according to their diel cycle (Duhamel et al. 2000 for fish DVM).  
496 Here the Chl *a* biomass peaked three months earlier and was low during the cruise. This area is  
497 considered highly dynamic with low residence time at local scale. However, it is located in the  
498 downstream recirculation area of the large PF meander as described in d'Ovidio et al. (2015)

499 supporting the development of a rich food web in this mesoscale retentive feature. As an indicator of  
500 high MM abundance and accessibility (Béhagle et al., 2017), the eastern slope of the Kerguelen Plateau  
501 is a well-known foraging area for top predators such as king penguins (*Aptenodytes patagonicus*),  
502 macaroni penguins (*Eudyptes chrysolophus*) and fur seals (*Arctocephalus gazella*), which  
503 predominantly forage within the SSL on crustaceans and myctophids (Bost et al., 2002, Lea and  
504 Dubroca 2003, Sato et al., 2004).

505

506 As hypothesized, low overall MM biomasses were reported in the low-chlorophyll upstream area,  
507 mainly due to low salp densities. West of the Plateau and south of the PF (M4), siphonophores  
508 dominated the total biomass while migrating euphausiids and myctophids (*K. anderssoni* and *E.*  
509 *antarctica*) were found in high densities in the SSL and jellyfish were significant in the deeper layers.  
510 The lowest overall biomass was found at the previous HNLC KERFIX station (Jeandel et al. 1998),  
511 located closer to the Plateau and north of the PF (M3). Here, gelatinous group (siphonophores, jellyfish  
512 and ctenophores) and fish (bathylagids and *Cyclothone* sp) exhibited a high diversity, crustacean  
513 abundance was low and fish also made a relatively high contribution to biomass. This particular  
514 community corresponded to warmer waters north of the PF delimiting the northern extent of the  
515 distribution area of the endemic Antarctic species *E. antarctica* (Duhamel et al., 2014). Upstream of the  
516 Plateau, the PF location is highly variable and undergoes a large seasonal change (Pauthenet et al.,  
517 2018). These authors reported that the PF is located at its southernmost position in March, i.e., during  
518 the survey period. As a consequence, the location of station M3 in relation to the PF may have shifted  
519 in the previous months and resulted in different physical and biogeochemical conditions. Moreover, the  
520 purported HNLC upstream area (especially at M4) presented similar levels of Chl *a* than the  
521 downstream M1 station. The spring-summer production at upstream stations was abnormally high  
522 when compared to the averaged Chl *a* in this area (Christaki et al., 2021), potentially influencing the  
523 densities of the MM populations and maybe partly blurring the effect of contrasting production  
524 regimes.

525

## 526 **2. Diel cycles and intra-station variability as sources of time varying patterns**

527 Despite clear differences in the vertical distribution of both acoustic densities and biomass-abundance  
528 between daytime and nighttime, a consistent three-layer system occurred over the whole study area  
529 from upstream to downstream regions of the Plateau. While higher total biomass was observed during  
530 nighttime, particularly in the surface layer, acoustic densities were remarkably similar between daytime  
531 and nighttime. This acoustic peculiarity was especially noticeable in the SSL where various densities

532 were reported at the two frequencies. Here, very few gelatinous organisms and fish were collected, and  
533 crustaceans dominated trawls during daytime. The combination of trawl avoidance during daylight and  
534 diurnal behaviour of myctophids could explain why their biomass were undersampled in the surface  
535 layer (Kaartvedt et al., 2012). Indeed, fish schooling is a diurnal behaviour leading to a patchy  
536 distribution during the day that vanishes at night (Saunders et al., 2013). The peak in acoustic densities  
537 above 100 m during daytime at both frequencies (particularly at 18 kHz) likely corresponded to a thin  
538 layer where small schools of myctophids occurred. This is supported by both previous acoustic  
539 measurements carried out in the area east of the Plateau corresponding to the station M1 (Behagle et  
540 al., 2017), and the diving depth of king penguins that feed mostly on *K. anderssoni* during daytime  
541 (Scheffer et al., 2016). Few fish species were caught in SSL during the day, with the shallow acoustic  
542 densities being likely *K. anderssoni* (Duhamel et al., 2000; Hunt and Swalding, 2021). The vertical  
543 distribution of this non-migratory species is based on age-segregation: juveniles are intensively feeding  
544 in the warm and productive surface waters while adults were found deeper (Lourenço et al., 2017).

545  
546 The diel cycle in the SSL was the largest contrast we observed, with the invasion of gelatinous,  
547 crustaceans and mesopelagic fish from mid- and deep layers to the epipelagic. The daily difference in  
548 biomass and in the RGB echograms evidenced the migratory pattern of numerous species, including *i*)  
549 salps, which were found deeper than 200 m in the morning and performed a first migration to  
550 subsurface at mid-day, before moving up to the surface layer at night (Nishikawa and Tsuda 2001,  
551 Henscke et al., 2021); *ii*) the main crustacean species, i.e. *E. vallentini* that performed DVM from  
552 subsurface-deep waters (100 m to 600 m depth) during daytime to the surface layer during nighttime  
553 (Mauchline and Fisher, 1969, Boden and Parker, 1986), and *T. gaudichaudii* that also displayed DVM  
554 through a more complex pattern due to an ontogenetic component, with juveniles moving in the upper  
555 100 m whereas adults descended to depths below 200 m during daytime (Pakhomov and Froneman,  
556 1999); and *iii*) the myctophid *E. antarctica* exhibited a typical DVM, occurring within the surface  
557 waters during the night and descending below 300 m during daytime, with a size component (larger  
558 individuals found deeper than 600 m at night, while small fish were located at 300-400 m during the  
559 day; Hulley and Duhamel, 2011). Other important contributors were non- or slightly migratory species,  
560 such as *K. anderssoni* (see above) and the siphonophore *R. plicata* that exhibited a quasi-permanent  
561 distribution below 300 m with minor diel movements (as suggested in Pugh 1984).

562  
563 Multiple layers and patches and diverse DVMs during the transition periods were observed on the RGB  
564 echograms. This bi-frequency visualization was particularly insightful to understand the vertical

565 patterns of averaged acoustic profiles that appeared relatively similar during both day and night  
566 periods. Here, we attempted to interpret this three-layer system based on the combination of bi-  
567 frequency responses and trawl sampling obtained during our survey and on the already known diel  
568 vertical distribution. During daytime, SSL was dominated by juveniles of *K. anderssoni* and of *T.*  
569 *gaudichaudii*, while this layer was invaded by numerous species at night from deeper waters, including  
570 salps, fish *E. antarctica*, and euphausiid *E. vallentini*. Preliminary results using the four-frequency  
571 comparison (but limited to the surface layer) indicated a more complex pattern with layers presenting  
572 multi-acoustic responses indicative of multi-species structures. During daytime, salps distributed in the  
573 upper part (~200 m) of MDL in the morning (patch observed on the RGB echogram in the downstream  
574 area), before moving up at mid-day, as indicated by a strong response at 18kHz (Wiebe et al., 2010). A  
575 mix of the main crustacean species (*E. vallentini* and adults *T. gaudichaudii* between 200 m and 300 m)  
576 was found on the Plateau. The lower part of the MDL was attributed to siphonophores collected below  
577 300 m, combined with crustaceans. During nighttime, crustaceans mainly migrated to the SSL, while  
578 siphonophores constituted a permanent layer below 300 m, moving slightly upward at night. Over the  
579 plateau, waters just above the bottom were characterized by a permanent layer that was found deeper  
580 (~600 m) at the other stations. During daytime in the DSL, this permanent 38kHz-dominated layer,  
581 centred at 600 m, was probably characterized by the main fish species in the area, i.e., large specimens  
582 of *E. antarctica*, adults of *K. anderssoni*, bathylagids and *Cyclothone* sp., together with siphonophores  
583 and euphausiids. During the night, a part of this fish community, probably juveniles or the smallest  
584 individuals, move upward together with euphausiids. However, a 600 m-depth layer remained  
585 permanently, with the same combination of organisms that was acoustically dominated by fish. The  
586 higher 38kHz acoustic levels compared to the 18kHz at the DSL could be due to this fish dominance,  
587 since larger non-migrant *E. antarctica* individuals have a reduced gaseous swimbladder relative to the  
588 smaller individuals that have a large air-filled swimbladder (Dornan et al. 2019). Other acoustic layers  
589 occurred deeper, at the limit of the 38kHz vertical range, where just two trawls were carried out, and  
590 reported a similar community with more deep-sea species such as jellyfish.

591  
592 The vertical patterns in biomass and communities together with the diel cycles were consistent between  
593 visits on the Plateau and in the upstream area. It suggested that the same MM populations were  
594 sampled at each station where a low horizontal transport occurred (Henschke et al., 2021). The  
595 occasional variability in biomass and abundance in the same layers could indeed be attributed either to  
596 the known MM patchiness (i.e., spatial variability) or to the development of trophic interactions (i.e.,  
597 temporal variability).

598

599 While the combination of trawl and acoustic sampling clearly benefited the description of the MM  
600 community, it is crucial to bear in mind the specificities of each methodology (Ariza et al., 2016).  
601 Despite the possibility of contamination of deep hauls by upper organisms due to the use of a non-  
602 closing trawl, we reduced this effect through fast launch and haul out during trawl operations.  
603 Moreover, while numerous species' were sampled, we only focused on the most abundant species. This  
604 precaution was particularly suitable in our study area where the dominant species were limited and  
605 represented a very high proportion of biomass and abundance, consequently contributing significantly  
606 to the backscatter. In turn, acoustic measurements were based on the properties of the dominant species  
607 in a volume containing many organisms, either in terms of relative backscatter intensity dominated by  
608 the strongest reflector or due to the frequency-dependent response. This implies that gas-bearing  
609 organisms, such as fish with air-filled swimbladders or siphonophores, dominated small fluid-like  
610 organisms at 18kHz and 38kHz (Ariza et al., 2016, Behagle et al., 2017).

611

612

### 613 **3. Variability in vertical distribution of carbon content and active flux associated with** 614 **macrozooplankton-micronekton.**

615 Although gelatinous groups dominated the wet biomass in the majority of trawls, organism energy  
616 content needs to be taken into account with respect to sustaining the development of higher trophic  
617 levels. For example, crustaceans are higher quality food than gelatinous organisms, such as salps  
618 (Harmelin-Vivien et al., 2019). Considering carbon content allows a better estimate of the relative  
619 contribution of the different groups in terms of their roles in the energy transfer along the food web.  
620 Mesopelagic fish represented the main source of carbon stock in the DSL. They were shown to play an  
621 important role in active transfer of carbon from the surface-intermediate layers to deep waters (Belcher  
622 et al., 2019). The extent of the active carbon flux driven by fish depends on the species composition,  
623 with not all species performing DVM (Romero-Romero et al., 2019, Klevjer et al., 2020). In our study,  
624 some of the highest fish carbon biomasses were measured at station M3, where relatively low  
625 abundances of crustacean were found in the upper layer (including zooplankton, see Hunt et al., this  
626 issue), potentially implying some top down control. However, primary productivity in surface waters at  
627 this upstream station was low, which may have contributed to the low crustacean biomass, and further,  
628 it is questionable whether such low biomass of fish can impact crustacean abundance (Pepin et al.,  
629 2013). Crustacean and gelatinous organisms represented a large, although varying, C stock on the  
630 Plateau, but they were not associated with high mesopelagic fish biomass, possibly due to depth

631 limitation (550 m depth over the shelf). For consistency, we used an average of water carbon content  
632 computed for each of the groups, based on available data from the literature. However, we  
633 acknowledge that variability can be observed between species of the groups and between different  
634 estimates within the same species. Such variability can be explained by the different geographic areas  
635 where the same species occurred and the samples obtained at different seasons, both potentially  
636 affecting the body composition of organisms (Schaafsma et al., 2018).

637

638 Additionally, we estimated the carbon flux mediated by migratory fish from the myctophid family, a  
639 major component in the Southern Ocean food web (Pakhomov et al., 1996; Saunders et al., 2019) and  
640 known to play an important role in the active transport of carbon to the deep ocean (Davison et al.,  
641 2013; Ariza et al., 2015; Belcher et al., 2019; Kwong et al., 2020). Due to sampling constraints and  
642 level of knowledge (see methods), myctophids were the group selected to estimate carbon over salps,  
643 euphausiids, or hyperiids, which represented higher biomass, at least according to the net trawling  
644 results (Fig. 3-8). Without discrediting the important role of the latter groups in the subantarctic food  
645 webs (Perissinoto et al., 1998; Pakhomov et al., 2002), it should be considered that our biomass data  
646 might be strongly affected by the catchability and selectivity performance of our trawling net (Meillat,  
647 2012, Béhagle et al., 2017). Myctophids are fast swimmers and they are expected to efficiently avoid  
648 trawling nets (Kaartvedt et al., 2012), especially when compared to quasi-drifting life forms like salps,  
649 or to smaller organisms such as euphausiids or hyperiids (Skjoldal, et al. 2013). Trawl avoidance can  
650 make a difference, considering that we used a net with a 65 m<sup>2</sup> mouth area. Hence, we presumed that  
651 myctophids were undersampled and are an important component of the DVM in the region, according  
652 to literature (Pakhomov et al., 1996; Saunders et al., 2019). This, along with the extraordinary  
653 migration extent of organisms, often beyond 700-800 m depth when they are larger than 40 mm  
654 (Badcock and Merret, 1976), made pertinent the estimation of carbon flux on this group. Interestingly,  
655 larger fish were sampled below the MLD over the Plateau. While they did not perform inter-zonal  
656 migration, they nonetheless contribute at a lower extent to the downward carbon flux as the acoustic  
657 backscatter during nighttime at this depth was not observed during daytime due to fish downward  
658 migration from SSL to deeper layers.

659

660 Our carbon flux estimation strongly relies on individual body mass and environmental temperature,  
661 using a respiration rate predictive equation (see methods). As discussed by Belcher et al. (2019),  
662 species-specific metabolism variance is not accounted for by this predictive equation and this should be  
663 added, along with the capture efficiency of the net, as factors potentially influencing our results.

664 Capture efficiency and metabolic models are a common source of uncertainty to estimate carbon flux in  
665 micronekton, and this might explain why results generated over the last two decades still differ by up to  
666 three orders of magnitude (see Table 5). Our respiratory carbon flux estimations, ranging from 0.001 to  
667 0.045 mg C m<sup>-2</sup> d<sup>-1</sup>, are for instance one order or magnitude lower than those obtained by Belcher et al.  
668 (2019) in the Atlantic sector of the Southern Ocean, using the same predictive equation, and based on  
669 non-corrected catch data, as we did (see Table 5). This demonstrates the urgent need to perform further  
670 inter-calibration experiments on micronekton samplers and acoustics (Pakhomov et al., 2010, Kaartvedt  
671 et al., 2012), and to work towards obtaining more accurate metabolic models for species involved in  
672 DVM (Belcher et al., 2019, 2020). In this study, the mesopelagos net is known to strongly undersample  
673 large fish (Meillat, 2012, Béhagle et al., 2017). Respiration is also expected to be underestimated in  
674 cold temperature environments, because the predictive equation was partially built from respiration  
675 rates calculated for temperate and tropical species (Belcher et al., 2020). Our active carbon flux values  
676 might therefore be underestimated to an unknown degree, and until these uncertainties are resolved, the  
677 results should be interpreted with caution in absolute terms. Indeed, the most recent inter-comparison  
678 of carbon fluxes between epi- and mesopelagic zones using a linear inverse ecosystem model suggested  
679 that estimates of zooplankton active transport using conservative estimates of standard metabolism are  
680 grossly underestimated (Kelly et al. 2020). Relative values among stations and visits were however  
681 revealing about how environmental factors and population dynamics can affect carbon flux. For  
682 instance, Figure 10 illustrates how carbon flux is strongly driven by the total migrant biomass, but that  
683 this biomass will be more efficiently converted into exported carbon when the size structure of the  
684 community is small. This results from higher metabolic rates for small fish (Equation 1). On the other  
685 hand, the migration range in small myctophid fishes smaller and shallower (Badcock and Merrett,  
686 1976), with significant implications when modelling fish-mediated carbon flux. Overall, the ocean-  
687 basin and slope-boundary stations M1 and M4, situated south off the PF, had greater migrant biomass,  
688 larger species, and twofold to threefold higher respiratory carbon fluxes. This highlights the importance  
689 of patchiness and community composition when assessing carbon flux, and demonstrate a strong  
690 bottom up structuring on the active component of the biological pump.

691

## 692 **Conclusion**

693 The complementary collection of trawl and acoustic data contribute to elucidate MM diversity, its  
694 complex horizontal and vertical organisation and the associated biogeochemical fluxes in the different  
695 primary production regimes in the Kerguelen region. While a consistent three-layers system has been  
696 determined between 12 m and 800 m over the Kerguelen seascape, the MM assemblage defined the



697 vertical patterns and its associated DVM. As expected, the highest biomasses of MM were found in  
698 productive areas on the Plateau and downstream. However, carbon content and flux from migrating  
699 myctophids, which contributed significantly to the carbon MM biomass, did not follow the same  
700 pattern. In order to obtain reliable active transport estimates of the different MM taxonomic groups,  
701 which are likely slightly to substantially underestimated, a comprehensive sampling effort should be  
702 deployed using multiple techniques: net samplings, acoustics, video imaging and genetics. The aim of  
703 this effort would be twofold, clarification of ecological diversity and biogeochemical basis of these  
704 organisms or ground truthing standing stocks for their sustainable management. The biophysical links  
705 also deserve urgent attention to enable describing the influence of physical features, such as the water  
706 mass stratification, the PF position at the Plateau and offshore areas, on pelagic food webs.

707

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Station	Visit	Date	Day/Night	Latitude (°S) /Longitude (°E)	Max depth (m)	Trawl ID	
M1	1st	08/03/18	Night	49.85 / 74.90	29-51	21	
		08/03/18	Night		248-290	22	
		08/03/18	Night		576-617	23	
		09/03/18	Day		367-400	24	
		09/03/18	Day		21-50	25	
		09/03/18	Day		611-632	26	
M2	1st	26/02/18	Day	50.62 / 72.00	318	1	
		26/02/18	Day		178-210	2	
		26/02/18	Day		329-350	3	
		27/02/18	Night		307-346	4	
		27/02/18	Night		35-55	5	
		27/02/18	Night		118-158	6	
	2nd	07/03/18	Day	151-170	15		
		07/03/18	Day	49-70	16		
		07/03/18	Day	315-350	17		
		07/03/18	Night	283-317	18		
		07/03/18	Night	30-50	19		
		07/03/18	Night	141-175	20		
	3rd	16/03/18	Night	33-65	37		
		16/03/18	Night	335-377	38		
		16/03/18	Night	21-30	39		
		17/03/18	Day	89-105	40		
		17/03/18	Day	318-340	41		
		17/03/18	Day	157-190	42		
	M3	1st	04/03/18	Day	50.68 / 68.06	29-55	13
			04/03/18	Day		423-460	14
2nd		15/03/18	Day	609-683	33		
		15/03/18	Night	591-610	34		
		15/03/18	Night	72-90	35		
		15/03/18	Night	368-415	36		
3rd		18/03/18	Day	772-814	43		
		18/03/18	Day	547-600	44		
		18/03/18	Day	47-65	45		
		19/03/18	Night	777-802	46		
	19/03/18	Night	611-650	47			

	19/03/18	Night		51-73	48
	01/03/18	Day	52.60 / 67.20	78-93	7
	01/03/18	Day		556-575	8
	01/03/18	Day		398-425	9
1st	02/03/18	Night		363-400	10
	02/03/18	Night		80-96	11
	02/03/18	Night		547-575	12
M4	14/03/18	Day		57-85	27
	14/03/18	Day		576-610	28
	14/03/18	Day		363-410	29
2nd	14/03/18	Night		572-600	30
	14/03/18	Night		52-80	31
	14/03/18	Night		365-400	32

969 Table 2. Proportion and occurrence of gelatinous species caught during trawl operations. Main  
 970 contributions are in bold (>50 % in occurrence and >3 % in relative frequency).

971

972

FAMILY	Species	% occurrence	% all stations	% M1	% M2	% M3	% M4
CHAETOGNATHS	<i>Sagitta gazellae</i>	<b>93.62</b>	0.77	0.43	0.62	3.56	1.34
CTENOPHORES	<i>Beroe cucumis</i>	31.91	0.89	0.75	0.21	2.33	2.95
	<i>Bolinopsis</i> sp.	29.79	0.74	0.24	0.09	<b>11.98</b>	0.09
	<i>Leucothea</i> sp.	2.13	0.01	0.00	0.00	0.17	0.00
MEDUSAE	<i>Atolla wyvillei</i>	17.02	1.53	0.62	0.00	<b>14.36</b>	<b>4.42</b>
	<i>Calyropsis borchgrevinki</i>	<b>51.06</b>	0.35	0.28	0.14	1.66	0.71
	<i>Calyropsis</i> sp. 2	6.38	0.02	0.00	0.00	0.31	0.00
	<i>Halicreas minimum</i>	2.13	0.00	0.00	0.00	0.05	0.00
	<i>Haliscera conica</i>	4.26	0.02	0.00	0.00	0.35	0.00
	Medusa unknown B	4.26	0.03	0.00	0.00	0.51	0.00
	<i>Periphylla periphylla</i>	29.79	1.02	0.05	0.19	<b>5.92</b>	<b>5.00</b>
	<i>Rhopalonema</i> sp.	2.13	0.01	0.00	0.00	0.00	0.05
	Scyphomedusae	2.13	0.05	0.00	0.00	0.00	0.40
	<i>Solmissus</i> sp. ( <i>Medusa unknown A</i> )	36.17	0.37	0.27	0.00	1.38	1.47
	<i>Stygiomedusa gigantea</i>	0.00	0.00	0.00	0.00	0.00	0.00
NEMERTEANS	<i>Pelagonemertes rollestoni</i>	8.51	0.01	0.00	0.00	0.20	0.00
POLYCHAETES	<i>Tomopteris carpenteri</i>	17.02	0.01	0.01	0.02	0.03	0.00
SALPS	<i>Salpa thompsoni</i>	<b>85.11</b>	<b>73.63</b>	<b>89.74</b>	<b>86.88</b>	<b>10.63</b>	<b>2.75</b>
SIPHONOPHORES	<i>Diphyes</i> sp.	4.26	0.00	0.00	0.00	0.01	0.00
	<i>Rosacea plicata</i>	<b>55.32</b>	<b>20.59</b>	<b>7.60</b>	<b>11.85</b>	<b>46.55</b>	<b>80.83</b>

973

974 Table 3. Proportion and occurrence of crustaceans species caught during trawl operations. Main  
 975 contributions are in bold (>50 % in occurrence and >3 % in relative frequency).  
 976

FAMILY	Species	% occurrence	% all stations	% M1	% M2	% M3	% M4
EUPHAUSIIDS	<i>Euphausia longirostris</i>	10.64	0.30	1.85	0.00	0.00	0.00
	<i>Euphausia triacantha</i>	<b>82.98</b>	<b>11.28</b>	<b>15.71</b>	<b>7.20</b>	<b>20.03</b>	<b>9.99</b>
	<i>Euphausia vallentini</i>	<b>87.23</b>	<b>43.12</b>	<b>43.28</b>	<b>28.16</b>	<b>41.55</b>	<b>74.39</b>
	<i>Thysanoessa macrura/vicina</i>	<b>51.06</b>	2.78	<b>4.99</b>	2.67	0.06	<b>3.30</b>
GAMMARID AMPHIPODS	<i>Cyphocaris richardi</i>	31.91	0.12	0.01	0.00	0.22	0.39
	<i>Danaela mimonectes</i>	10.64	0.01	0.00	0.00	0.01	0.02
	<i>Eurythenes obesus</i>	6.38	0.00	0.01	0.00	0.01	0.00
	<i>Eusiroides stenopleura</i>	19.15	0.03	0.02	0.00	0.10	0.07
	<i>Parandania boeckii</i>	40.43	0.89	1.55	0.08	2.22	1.11
	HYPERIID AMPHIPODS	<i>Cylopus magellanicus</i>	<b>80.85</b>	0.87	2.27	0.89	0.25
<i>Hyperia spinifera</i>		12.77	0.01	0.01	0.01	0.01	0.00
<i>Hyperia macrocephala</i>		6.38	0.00	0.00	0.01	0.00	0.00
<i>Hyperiella antarctica</i>		21.28	0.01	0.01	0.01	0.03	0.01
<i>Hyperoche luetkenides</i>		44.68	0.07	0.11	0.09	0.03	0.02
<i>Pegohyperia princeps</i>		2.13	0.00	0.00	0.00	0.00	0.00
Physosomata sp. 1		6.38	0.00	0.00	0.00	0.02	0.00
Physosomata sp. 2		4.26	0.00	0.01	0.00	0.00	0.00
<i>Primno macropa</i>		<b>87.23</b>	1.65	2.07	1.52	<b>3.44</b>	0.44
Scinidae sp.		0.00	0.00	0.00	0.00	0.00	0.00
<i>Themisto gaudichaudii</i>		<b>100.00</b>	<b>37.77</b>	<b>25.49</b>	<b>59.06</b>	<b>29.42</b>	<b>9.68</b>
<i>Vibilia antarctica</i>		<b>72.34</b>	0.59	2.44	0.25	0.40	0.05
MYSIDS	<i>Neognathophausia gigas</i>	8.51	0.01	0.00	0.00	0.04	0.00
	Mysida sp.	17.02	0.25	0.00	0.05	1.44	0.00
	Mysida sp. (red)	4.26	0.04	0.00	0.00	0.27	0.00
NATANTIA	<i>AcanthePHYra pelagica</i>	4.26	0.00	0.00	0.00	0.01	0.00
	<i>Campylonotus</i> sp. (red)	21.28	0.01	0.02	0.00	0.03	0.00
	<i>Pasiphaea scotiae</i>	25.53	0.04	0.03	0.00	0.08	0.09
	<i>Gennada</i> sp./ <i>Natantia</i> sp.	6.38	0.01	0.01	0.00	0.03	0.00
	Sergestidae sp.	6.38	0.01	0.03	0.00	0.00	0.00
	Decapoda larvae	10.64	0.01	0.02	0.00	0.02	0.00
OSTRACODS	<i>Gigantocypris muelleri</i>	21.28	0.10	0.07	0.00	0.30	0.19

977

978 Table 4. Proportion and occurrence of fish species caught during trawl operations. Main contributions  
 979 are in bold (>40 % in occurrence and >3 % in relative frequency).  
 980

FAMILY	Species	% occurrence	% all stations	% M1	% M2	% M3	% M4
BATHYLAGIDAE	<i>Bathylagus tenuis</i>	23.40	<b>5.52</b>	<b>3.58</b>	0.00	<b>7.94</b>	<b>4.69</b>
GONOSTOMATIDAE	<i>Cyclothone</i> sp. A	25.53	<b>3.18</b>	0.68	0.00	2.65	<b>6.93</b>
	<i>Cyclothone</i> sp. B	2.13	0.06	0.00	0.00	0.13	0.00
STOMIIDAE	<i>Stomias boa/gracilis</i>	21.28	0.83	1.87	0.00	0.97	0.22
ASTRONESTHIDAE	<i>Borostomias antarcticus</i>	2.13	0.03	0.00	0.00	0.06	0.00
IDIACANTHIDAE	<i>Idiacanthus atlanticus</i>	2.13	0.03	0.17	0.00	0.00	0.00
SCOPELARCHIDAE	<i>Bentalbella macropinna</i>	8.51	0.18	0.17	0.00	0.06	0.45
PARALEPIDIDAE	<i>Notolepis coatsi</i>	<b>48.94</b>	<b>3.03</b>	1.70	<b>12.20</b>	1.87	2.46
MYCTOPHIDAE	<i>Electrona antarctica</i>	<b>65.96</b>	<b>27.71</b>	<b>29.64</b>	<b>37.50</b>	<b>17.62</b>	<b>40.22</b>
	<i>Electrona subaspera</i>	2.13	0.03	0.17	0.00	0.00	0.00
	<i>Gymnoscopelus bolini</i>	2.13	0.03	0.00	0.00	0.06	0.00
	<i>Gymnoscopelus braueri</i>	<b>44.68</b>	<b>4.07</b>	<b>3.24</b>	2.68	<b>5.62</b>	2.46
	<i>Gymnoscopelus fraseri</i>	4.26	0.27	0.00	0.60	0.00	0.78
	<i>Gymnoscopelus nicholsi</i>	14.89	0.27	0.17	1.79	0.06	0.11
	<i>Krefflichthys anderssoni</i>	<b>55.32</b>	<b>28.10</b>	<b>20.61</b>	<b>18.15</b>	<b>41.06</b>	<b>14.30</b>
	<i>Krefflichthys anderssoni</i> (postlarvae)	<b>55.32</b>	<b>21.18</b>	<b>32.54</b>	<b>4.17</b>	<b>18.85</b>	<b>24.13</b>
	<i>Nannobranchium achirus</i>	8.51	0.39	0.00	0.00	0.65	0.34
	<i>Protomyctophum andriashevi</i>	4.26	0.12	0.68	0.00	0.00	0.00
	<i>Protomyctophum bolini</i>	38.30	1.54	1.19	<b>6.55</b>	0.19	2.23
	<i>Protomyctophum gemmatum</i>	2.13	0.03	0.17	0.00	0.00	0.00
	<i>Protomyctophum parallelum</i>	4.26	0.06	0.00	0.00	0.13	0.00
	<i>Protomyctophum tenisoni</i>	19.15	0.45	0.85	2.38	0.13	0.00
	Myctophidae (postlarvae)	4.26	0.09	0.00	0.00	0.19	0.00
MURAENOLEPIDAE	<i>Muraenolepis marmoratus</i>	27.66	0.83	0.51	<b>5.95</b>	0.26	0.11
MACROURIDAE	Macrouridae sp.	2.13	0.03	0.00	0.00	0.06	0.00
MELANONIDAE	<i>Melanonus gracilis</i>	4.26	0.12	0.51	0.00	0.06	0.00
MELAMPHAIDAE	<i>Poromitra crassiceps</i>	2.13	0.33	0.00	0.00	0.71	0.00
LIPARIDAE	<i>Paraliparis thalassobathyalis</i>	2.13	0.03	0.00	0.00	0.06	0.00
NOTOTHENIIDAE	<i>Notothenia rossii</i> (blue fingerling)	10.64	0.18	0.00	0.89	0.19	0.00
	Postlarvae type A	25.53	0.95	1.53	<b>6.55</b>	0.06	0.00
GEMPYLIDAE	<i>Paradiplospinus gracilis</i>	4.26	0.06	0.00	0.60	0.00	0.00
ACHIROPSETTIDAE	<i>Achiropsetta tricholepis</i>	6.38	0.12	0.00	0.00	0.26	0.00
	Larvae (unidentified)	6.38	0.18	0.00	0.00	0.06	0.56

982 Table 5. Comparison of migrant biomass (MB), respiratory carbon flux (RCF) and total carbon fluxes  
 983 (TCF) estimated in this study and in other regions for myctophids (except in Kwong et al. (2020)  
 984 estimation for micronekton including myctophids, decapods, and cephalopods). Mechanism included to  
 985 compute the TCF are annotated with the following letters: R (respiration), D (defecation), E  
 986 (excretion), and M (mortality). Temperature refers to the residence depth of myctophids during daytime  
 987 according to the authors.  
 988

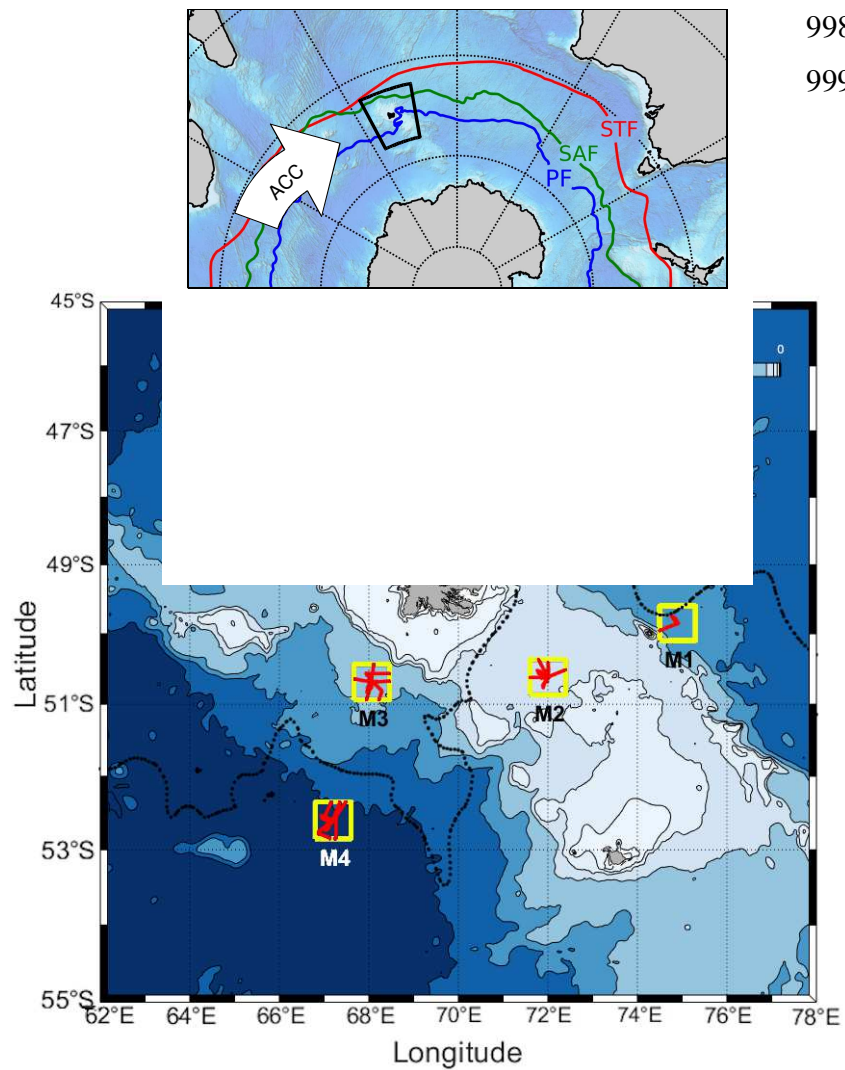
Source	Location	Temperature (°C)	Site	MB (mg C m <sup>-2</sup> d <sup>-1</sup> )	RCF (mg C m <sup>-2</sup> d <sup>-1</sup> )	TCF (mg C m <sup>-2</sup> d <sup>-1</sup> )
This study <sup>a§</sup>	Kerguelen Islands	2.2	Productive downstream (M1)	14.676	0.043	0.087 <sup>RDM</sup>
		2.2	Productive on Plateau (M2)	1.761 (0.041 - 5.987)	0.004 (0.001 - 0.012)	0.009 (0.001 - 0.026) <sup>RDM</sup>
		2.2	HNLC upstream, north of PF (M3)	1.255 (0.201 - 2.309)	0.005 (0.001 - 0.008)	0.009 (0.002 - 0.016) <sup>RDM</sup>
		2.2	HNLC upstream, south of PF (M4)	10.072 (5.067 - 15.077)	0.031 (0.016 - 0.045)	0.061 (0.032 - 0.091) <sup>RDM</sup>
Kwong et al. (2020) <sup>a§</sup>	Southeast Australia	10-20	Cold core eddy "B-CCE"	0.5	0.17	0.38 <sup>RDM</sup>
		10-20	Warm core eddy "R-WCE"	4.1	0.56	1.53 <sup>RDM</sup>
		10-20	Warm core eddy "WCE"	10.6	2.75	6.71 <sup>RDM</sup>
Belcher et al. (2019) <sup>a§</sup>	Scotia Sea	2	JR 161 WSS	49.8	0.05	-
		2	JR161 NSS	520.6	0.28	-
		2	JR177 GB	238.5	0.13	-
		2	JR177 MSS	407.1	0.33	-
Ariza et al. (2015) <sup>b†</sup>	Canary Islands	12	North of Gran Canaria	168	2.68	-
Hudson et al. (2014) <sup>b†</sup>	North Azores	6.6	Reykjanes Rdige	5.2	0.005-0.027	-
		11.8	Azorean Zone	40	0.046-0.271	-
Hidaka et al. (2001) <sup>b§</sup>	Western equatorial Pacific	9.3	Station 15	462.5	1.98	2.16 <sup>RDM</sup>
		9.3	Station 16	248.9	1.06	1.17 <sup>RDM</sup>
		9.3	Station 8	539.5	2.31	2.53 <sup>RDM</sup>
		9.3	Station 10	406.5	1.74	1.90 <sup>RDM</sup>
		9.3	Station 13	726.92	3.07	3.36 <sup>RDM</sup>

<sup>a</sup>Uncorrected for capture efficiency  
<sup>b</sup>Assumes 14% of capture efficiency  
<sup>†</sup>Small framed trawl  
<sup>‡</sup>Medium framed trawl  
<sup>§</sup>Large pelagic trawl

989

990

991 Fig. 1. Location of the study area in the polygon (black line) with the main oceanographic features, i.e.  
992 the Antarctic circumpolar current (ACC) and the main circumpolar fronts, the polar front (PF), the  
993 subantarctic front (SAF) and the Subtropical front (STF) (upper panel), and locations of the four  
994 stations (M1, M2, M3 and M4) in the Kerguelen region during the MOBYDICK survey (lower panel).  
995 Acoustic and trawl data areas are indicated by blue squares. The dotted line indicates the mean location  
996 of the Polar Front during the study period.  
997

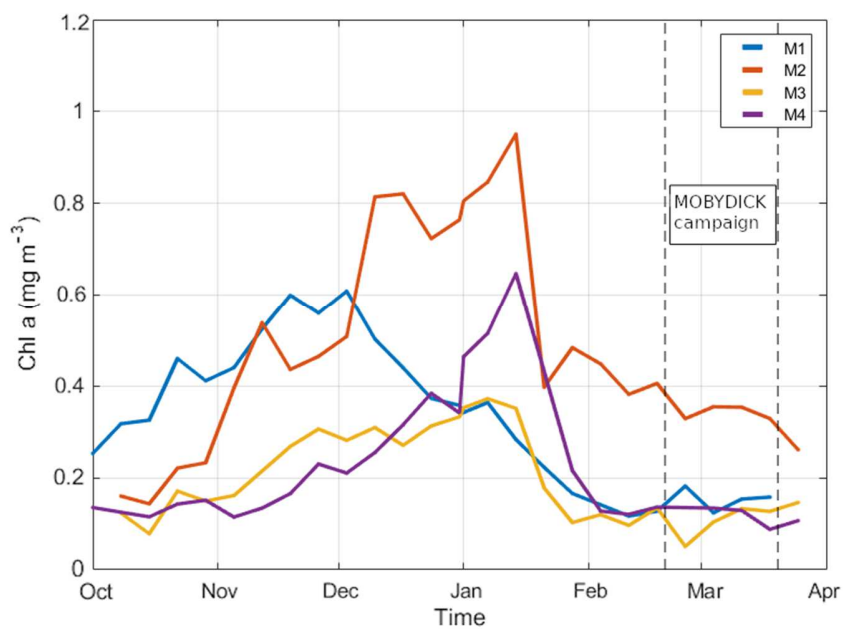


998

999

1000 Fig. 2. Time series of weekly-averaged chlorophyll a concentration ( $\text{mg m}^{-3}$ ) at each MOBYDICK  
1001 station (blue squares in Figure 1) from October 2017 to March 2018.

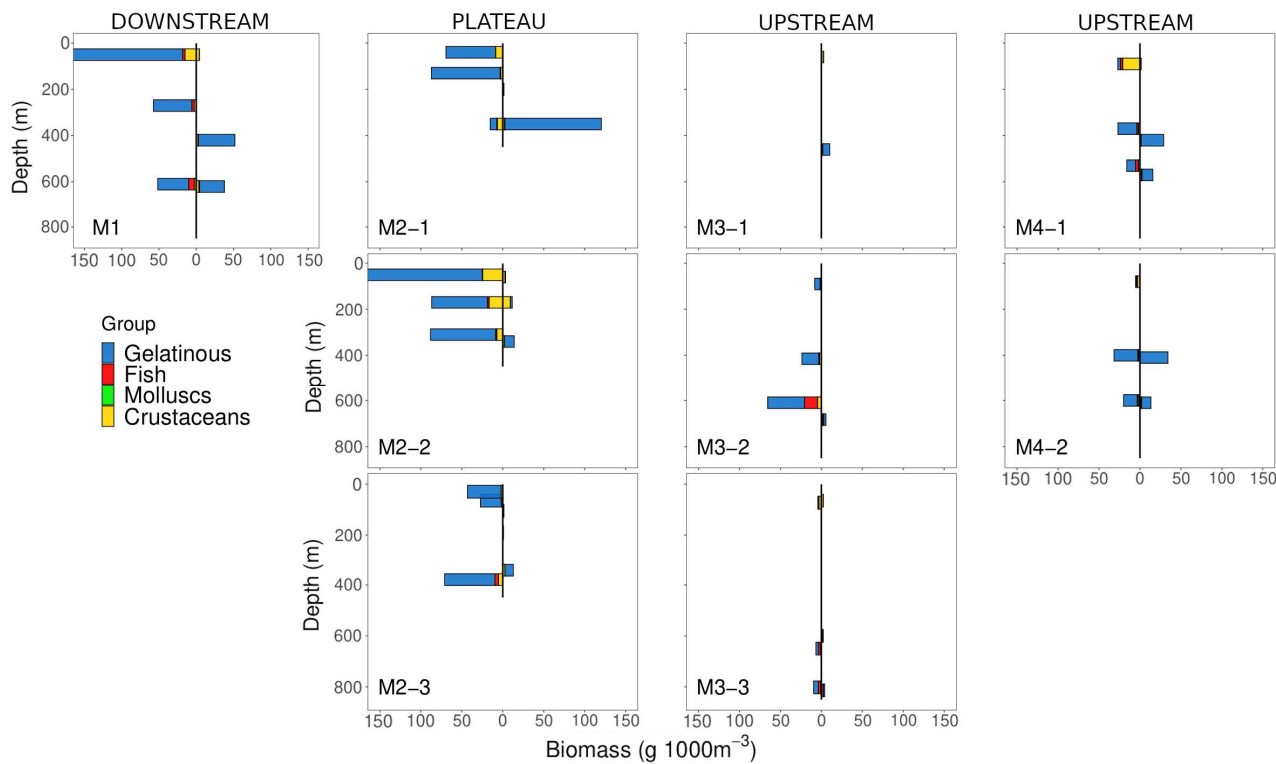
1002  
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1004





1005 Fig. 3. Night-day (left-right) absolute wet biomass (in  $\text{g } 1000 \text{ m}^{-3}$ ) of macrozooplankton-micronekton  
 1006 from trawls.

1007

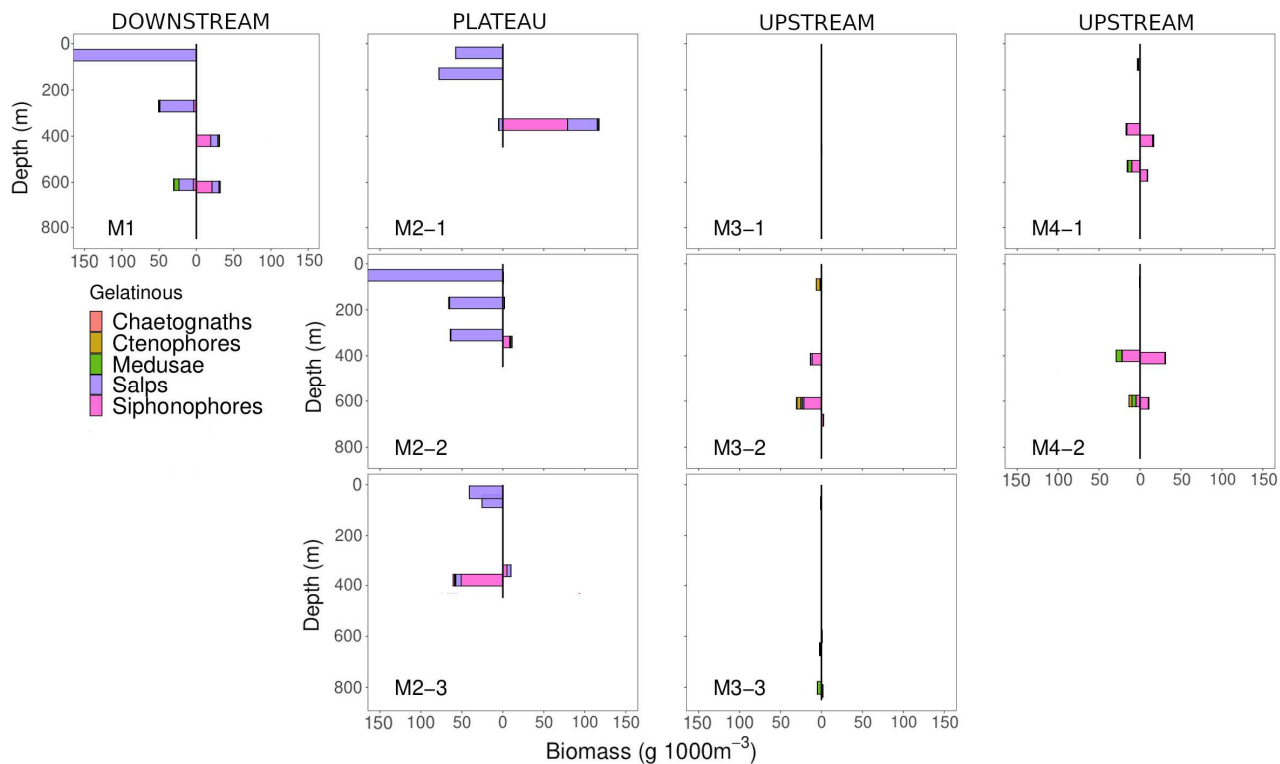


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1009

1010 Fig. 4. Night-day (left-right) absolute wet biomass (in g 1000 m<sup>-3</sup>) of the main gelatinous organisms  
 1011 from trawls.

1012

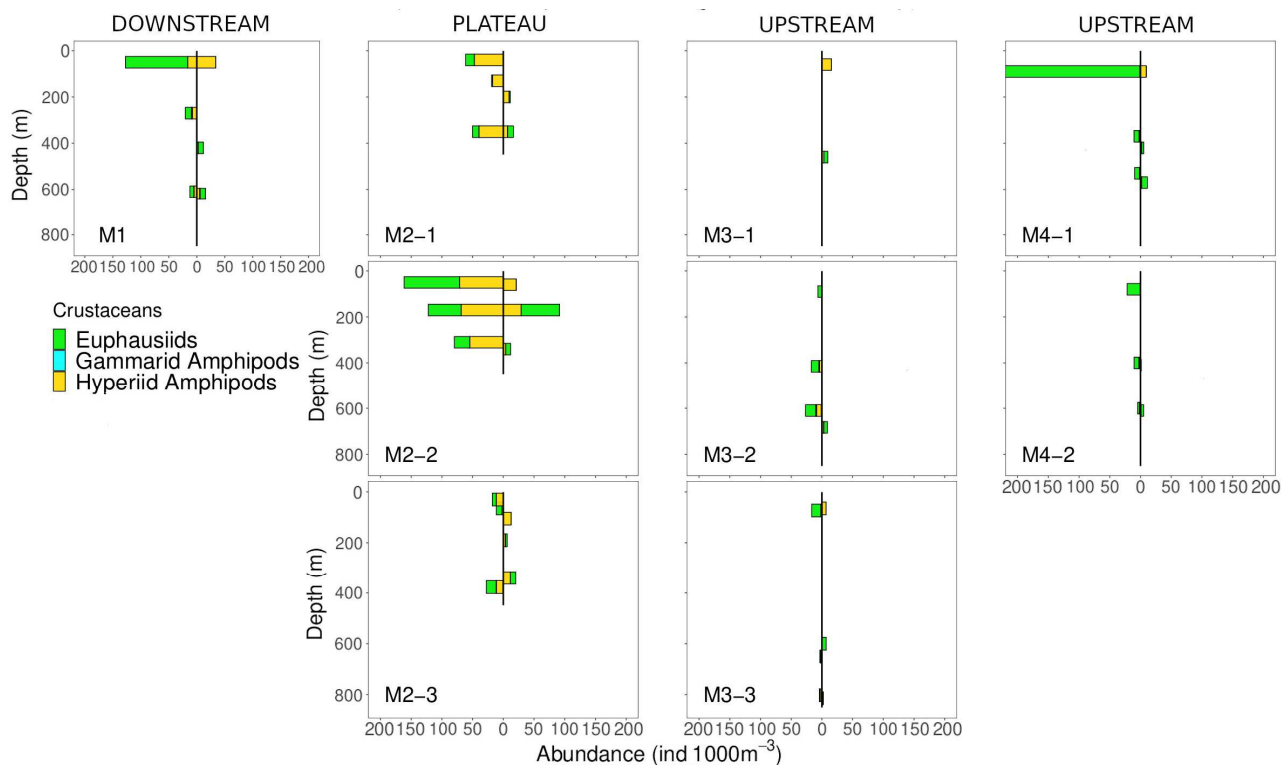


1013

1014

1015 Fig. 5. Night-day (left-right) absolute abundance (in individual 1000 m<sup>-3</sup>) of the main crustaceans from  
1016 trawls.

1017

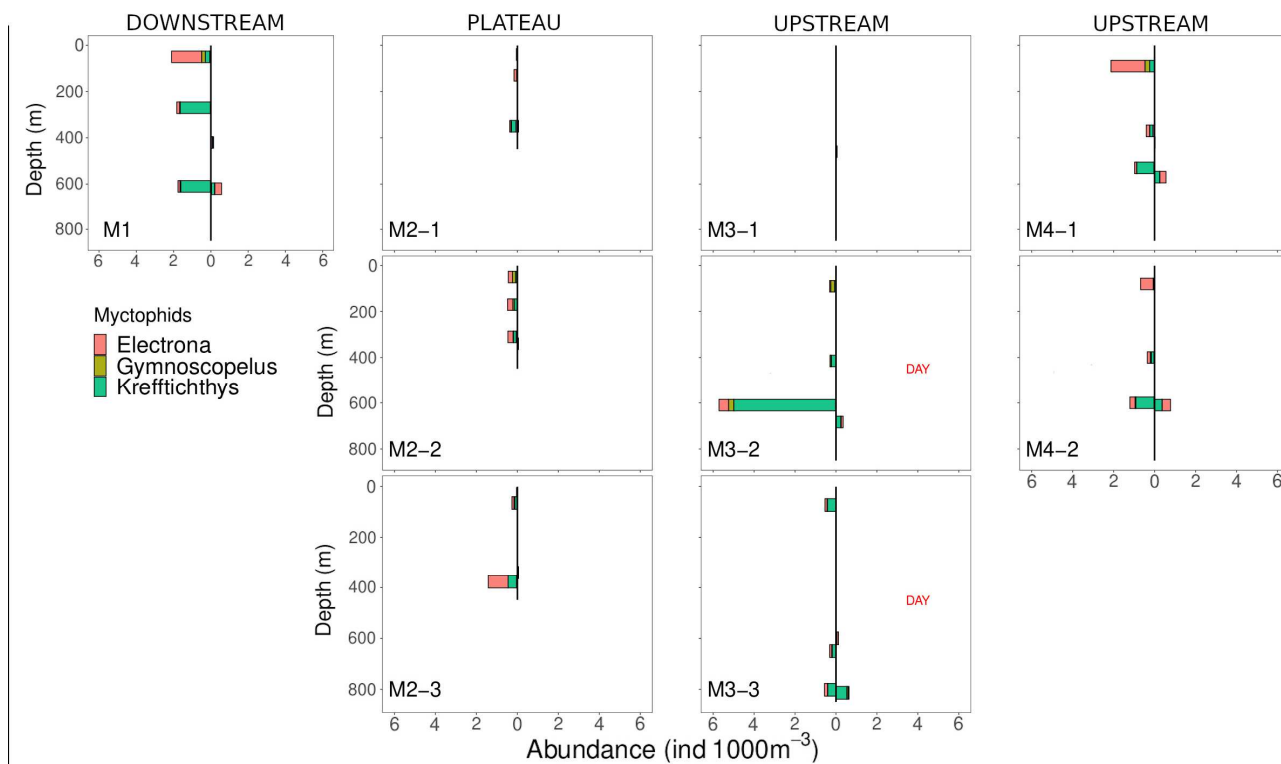


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1019

1020 Fig. 6. Night-day (left-right) absolute abundance (in individual 1000 m<sup>-3</sup>) of the main myctophids from  
1021 trawls.

1022

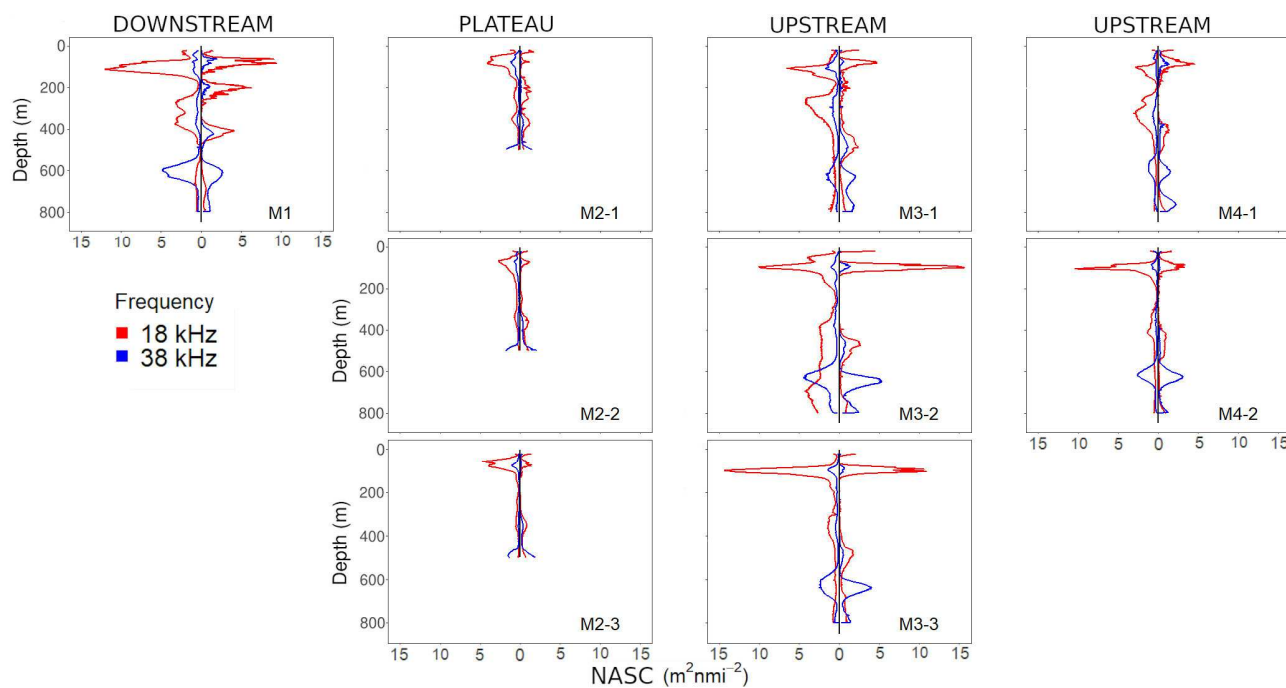


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1024

1025 Fig. 7. Night-day (left-right) mean vertical NASC profiles at 18kHz (red) and 38 kHz (blue).

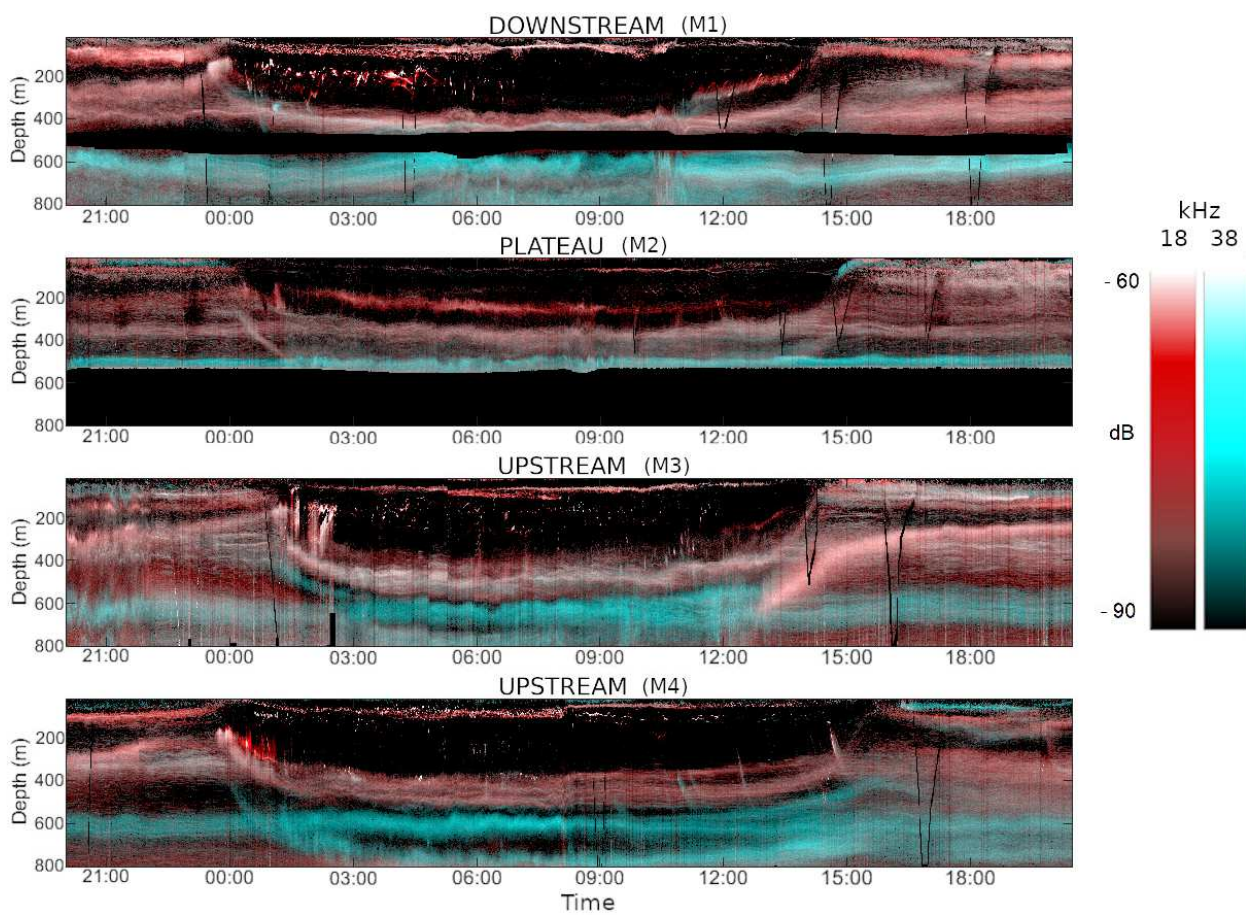
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1028

1029 Fig. 8. Daily RGB composites of Sv values (dB re 1m<sup>-1</sup>) from 12 to 800m for the four stations, with  
1030 the 18 kHz displayed in red and the 38 kHz frequency displayed both in green and blue.  
1031

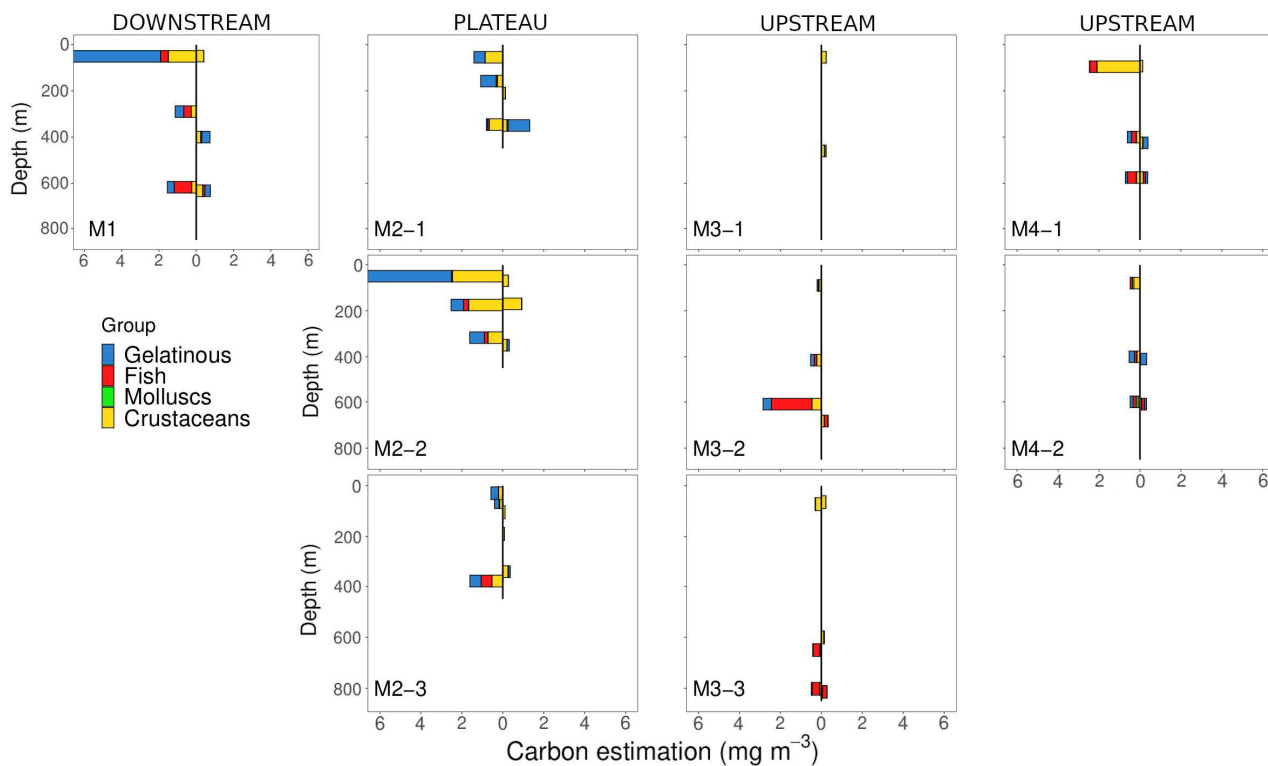


1032

1033

1034 Fig. 9. Night-day (left-right) carbon content (in  $\text{mg m}^{-3}$ ) of macrozooplankton-micronekton from  
1035 trawls.

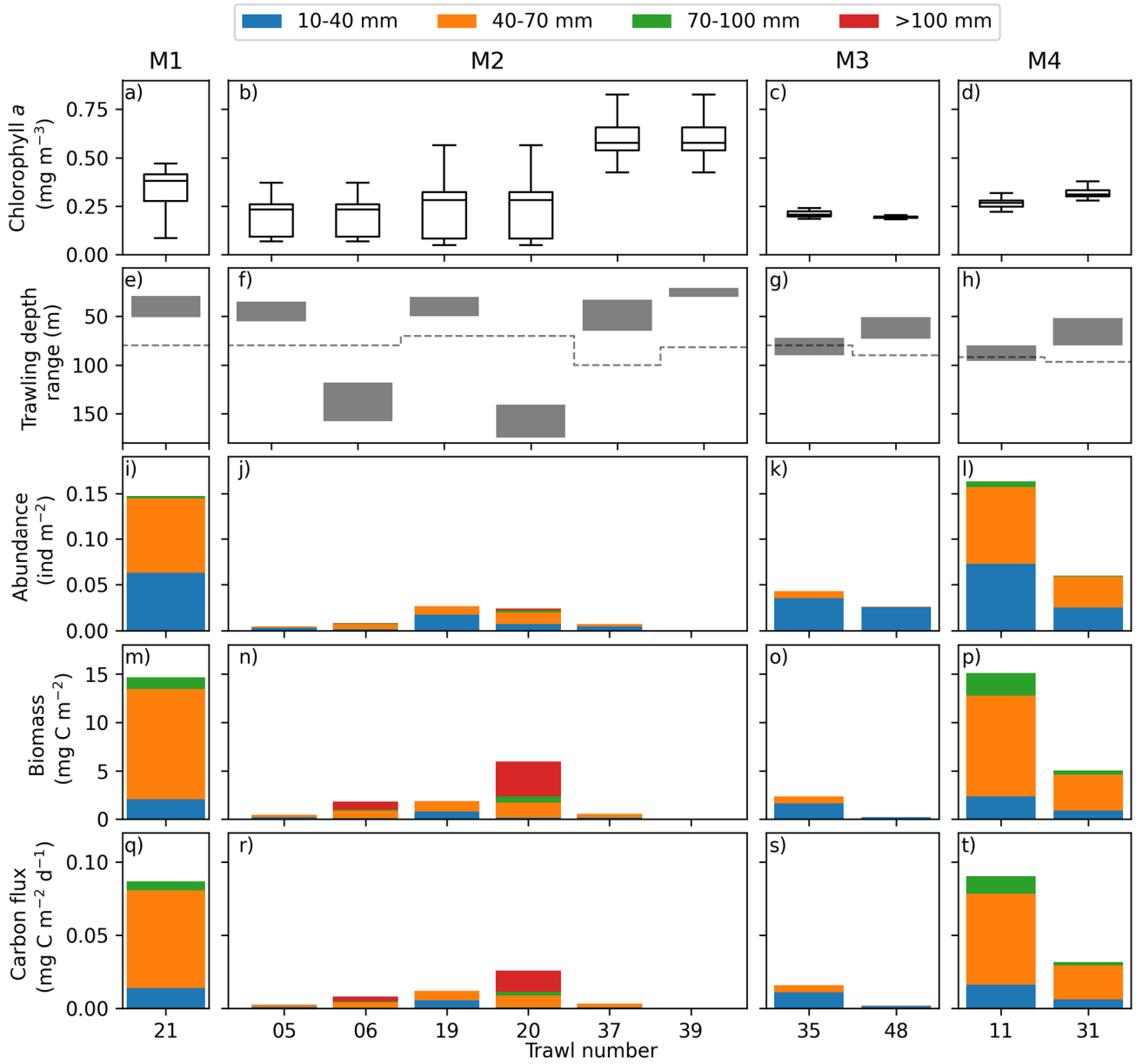
1036



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1038

1039 Fig. 10. Averaged chlorophyll *a* from 20 to 100 m depth (a-d), depth range of trawling used to target  
 1040 the migrant layers in the 200 m surface scattering layer (grey boxes) and mixed layer depth (dashed  
 1041 line) at each visit (e-h), and migrant abundance (i-j), biomass (m-p) and carbon flux (q-t) mediated by  
 1042 fish from the family Myctophidae, through respiration, defecation, and mortality at depth.  
 1043



1044