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1 A novel animal-borne miniature echosounder to observe the distribution and migration  
2 patterns of intermediate trophic levels in the Southern Ocean

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12 Highlights:

13 - A novel sonar tag provides an acoustic scan of the elephant seal environment

14 - The sonar tag is able to detect common features such as the diel vertical migration of small  
15 organisms

16 - Contrasting oceanographic conditions affect the vertical distribution and abundance of mid-  
17 trophic level organisms

18 - Areas of high particle abundances were observed over 500 m, potentially corresponding to  
19 marine snow events

20 Abbreviations:

21 DSL: Deep-Scattering Layer, DVM: Diel Vertical Migration, FPCA: Functional Principal  
22 Component Analysis, KER: Kerguelen Islands, PV: Peninsula Valdes, MTL: Mid-Trophic  
23 Level, NSAF: Northern Sub-Antarctic Front, PCAs: Prey Capture Attempts, SAF: Sub-  
24 Antarctic Front, SO: Southern Ocean

25

26 Abstract

27 Despite expanding *in-situ* observations of marine ecosystems by new-generation sensors,  
28 information about intermediate trophic levels remains sparse. Indeed, mid-trophic levels,  
29 while encompassing a broad range of zooplankton and micronekton organisms that represent

30 a key component of marine ecosystems and sustain large and diverse communities of marine  
31 predators, are challenging to sample and identify. In this study, we examined whether an  
32 animal-borne miniature active echosounder can provide information on the distribution and  
33 movements of mid-trophic level organisms. If so, such a sonar tag, harnessing the persistent  
34 diving behaviour of far-ranging marine mammals, could greatly increase the density of data  
35 on this under-studied biome. High-frequency (1.5 MHz) sonar tags were deployed  
36 simultaneously with oceanographic tags on two southern elephant seals (*Mirounga leonina*),  
37 at the Kerguelen Islands and Valdés Peninsula (Argentina), and recorded acoustic backscatter  
38 while the seals foraged respectively in the Indian and the Atlantic sectors of the Southern  
39 Ocean. The backscatter varied widely over time and space, and the seals attempted to capture  
40 only a small fraction of the insonified targets. Diel vertical migration patterns were clearly  
41 identifiable in the data, reinforcing our confidence in the ability of the sonar tags to detect  
42 living mid-trophic organisms along with possibly sinking biological detritus. Moreover, CTD  
43 tags attached to the same animals indicated how the abundance, size distribution, and diel  
44 migration behaviour of acoustic targets varied with water bodies. These preliminary results  
45 demonstrate the potential for animal-borne sonars to provide detailed *in-situ* information.  
46 Further validation effort will make it a valuable tool to refine the estimation of carbon export  
47 fluxes as well as for assessing the variation of mid-trophic level biomass according to  
48 oceanographic domains and seasons.

49 Keywords: sonar tag, diel vertical migration, micronekton, marine acoustics, biologging,  
50 functional data analysis.

51

## 52 **Introduction**

53 Marine ecosystems are manifesting multi-level responses to oceanographic changes related to  
54 global warming, from a suspected shift in phytoplankton communities (Montes-Hugo *et al.*  
55 2009, Barton *et al.* 2016) to top-predator population-size variations (Bost *et al.* 2015,  
56 Sydeman *et al.* 2015). However, assessment of the biological consequences of a changing  
57 ocean is hampered by a scarcity of information on the intermediate or mid-trophic levels  
58 (MTLs) (Hidalgo and Browman 2019). The crucial MTLs linking phytoplankton to upper

59 marine predators are composed of zooplankton and micronekton (e.g. mesopelagic fishes and  
60 squids, euphausiids, siphonophores) (Handegard et al. 2009, Escobar-Flores et al. 2018)  
61 presenting a wide range of body structures (e.g. crustaceans with a chitinous exoskeleton,  
62 bony or gelatinous organisms), sizes (from a few millimetres for euphausiid larvae to a meter  
63 for some siphonophores) and behaviours (e.g. planktonic or nektonic) (Sutton 2013, St. John  
64 et al. 2016, Kloser et al. 2016). The mesopelagic biome, comprising a third of the global-  
65 ocean volume, is one of the largest but least-known marine habitats (Reygondeau *et al.* 2018),  
66 and considerable uncertainties remain regarding the total biomass of mesopelagic fishes.  
67 Estimates of this biomass range from 2 to 20 gigatons (Irigoien *et al.* 2014, Kloser *et al.* 2016,  
68 Proud *et al.* 2019), the latter being some 100 times the annual catch of all existing fisheries (  
69 Anderson *et al.* 2019, Hidalgo and Browman 2019). The resulting scantiness of information  
70 on the structure and turnover of mesopelagic food webs hinders accurate predictions about the  
71 consequences of environmental changes or industrial fishing on this biome, and on the  
72 numerous higher-level predators that it supports.

73  
74 Information about the distribution and composition of MTLs is also critical for improved  
75 estimates of carbon export fluxes. The Southern Ocean (SO) in particular plays a crucial role  
76 in carbon sequestration, accounting for approximately 40% of global anthropogenic CO<sub>2</sub>  
77 uptake (DeVries 2014). The biological carbon pump operating in the SO remains only  
78 partially explained due to the difficulty in monitoring its biotic environment, although recent  
79 programmes such as KEOPS or CROZEX have proposed, in some parts of the SO, a  
80 quantification of biological processes leading to carbon export (Blain *et al.* 2007, Pollard *et*  
81 *al.* 2009, Salter *et al.* 2012, Le Moigne *et al.* 2016). The biological carbon pump begins with  
82 primary production performed by phytoplankton, which represents the main source of organic  
83 carbon exported to mesopelagic layers (Buesseler *et al.* 2007). Gravitational sinking of

84 phytoplankton as individual cells and aggregates is responsible for a significant portion of  
85 carbon export in the SO (Leblanc *et al.* this issue, Laurenceau-Cornec *et al.* 2015a). However,  
86 alternative biological mechanisms transporting the carbon trapped by phytoplankton to deep  
87 waters are still poorly understood as they are likely to rely mainly on the behaviour of MTLs.

88 Of particular note with regard to MTL behaviour is the phenomenon of diel vertical migration  
89 (DVM), which is performed by a large majority of MTL organisms, from small zooplanktonic  
90 organisms to mesopelagic fish (Hays 2003, Sims *et al.* 2006, Watanabe *et al.* 2006), and is  
91 found across all oceans (Behrenfeld *et al.* 2019). Representing the largest daily migration  
92 observed in the biosphere (Brierley 2014), and presenting differences in migration patterns  
93 depending on both the species and its life stage (Atkinson *et al.* 1992), DVM participates in a  
94 massive carbon transfer across the mixed layers of the ocean (Buesseler and Boyd 2009,  
95 Cavan *et al.* 2015, Aumont *et al.* 2018, Hernández-León *et al.* 2020). This vertical migration  
96 pump results from MTL zooplankton and micronekton rising to the euphotic zone near the  
97 surface where they generally feed at night. Carbon acquired at the surface is then actively  
98 transported during the day to deeper waters where MTLs release rapidly-sinking faecal pellets  
99 that form large aggregates (Belcher *et al.* 2017). This biological detritus gravitational flux, in  
100 addition to active transport by MTL organisms, increases the transfer and transformation of  
101 carbon (Cavan *et al.* 2015, Belcher *et al.* 2017, Cavan *et al.* 2019b), and contributes directly  
102 to deep carbon sequestration. Preliminary estimates suggest that MTLs may be responsible for  
103 about a quarter of carbon transport to deeper waters, though large uncertainties persist and  
104 regional variability exists (Boyd *et al.* 2019). Achieving better quantification of the role  
105 played by MTLs in the biological carbon pump is therefore still one of the current challenges  
106 in oceanography.

107 Although advances in marine acoustics, especially in multi-frequency and multi-beam  
108 echosounders, have resulted in a coarse classification of micronektonic organisms (Escobar-

109 Flores *et al.* 2019), the understanding of MTL taxonomic composition, biomass, and  
110 behaviour remains limited due to the difficulty of sampling. This is especially true for the SO  
111 where logistics and weather constrain ship-based operations. Consequently, acoustic and net-  
112 tow surveys of the mesopelagic layer, such as krill stock monitoring surveys (Fielding *et al.*  
113 2014, Tarling *et al.* 2018, Manno *et al.* 2020), remain sparse for most SO sectors. In addition,  
114 although such surveys are highly valuable, they inevitably suffer from limited spatial and  
115 temporal coverage (Kloser *et al.* 2009). Each method also has its own sources of bias.  
116 Acoustic surveys are sensitive to regional differences in the relative abundance of  
117 mesopelagic species or in their body structure (Dornan *et al.* 2019). Net-tow sampling, which  
118 is often used to validate hydroacoustic surveys, suffers from an underestimation of energetic  
119 mesopelagic fishes that are able to escape the trawl (Kaartvedt *et al.* 2012, Proud *et al.* 2019),  
120 and rarely has sufficient spatial resolution to reveal mesoscale structuring (Davison *et al.*  
121 2015). Although continuous ship-based acoustic surveys can sample over these larger spatial  
122 scales, they generally lack simultaneous sampling of fine-scale *in-situ* oceanographic profiles  
123 to investigate the coupling between physical and biological processes (Proud *et al.* 2019).  
124

125 Helping to fill in the gaps left by ship-based surveys are autonomous ocean profilers (e.g.  
126 ARGO profilers and gliders), whose development has enabled extensive sampling of the  
127 physical properties of the water column. Recently some profilers were equipped to make  
128 continuous recordings of acoustic backscatter (Haëntjens *et al.* 2020). However, the relatively  
129 slow vertical movement of autonomous underwater robotic samplers may prevent reliable  
130 sampling of more rapid biological processes, such as the daily vertical migration of actively  
131 swimming larger-size micronekton species.

132 A creative approach to achieve dense sampling of physical oceanographic parameters in  
133 otherwise difficult-to-observe oceanographic regions has been to fit marine animals with

134 multi-sensor biologging tags so that they become ocean samplers (Fedak 2004, Hindell *et al.*  
135 2016, Harcourt *et al.* 2019). Although this method does not provide systematic surveys, it  
136 offers the important advantage of providing simultaneous information about marine predator  
137 foraging ecology along with oceanographic conditions such as temperature, salinity or light  
138 level (Biuw *et al.* 2007, Guinet *et al.* 2014).

139 Biologging tags with sensors for temperature, salinity, chlorophyll-*a* concentration, and  
140 dissolved oxygen have yielded fine-scale descriptions of oceanic processes in remote areas  
141 (Roquet *et al.* 2013, Bayle *et al.* 2015, Bailleul *et al.* 2015). Southern elephant seals  
142 (*Mirounga leonina*, SES hereafter) are particularly useful for such sampling as they perform  
143 long-range foraging trips with continuous diving to mesopelagic depths, routinely reaching  
144 1000 m and in rare cases exceeding 2000 m (Roquet *et al.* 2009, Hindell *et al.* 2016). In  
145 recent years, animal-borne sensors have been developed to quantify the marine organisms  
146 encountered by deep-diving mammals. High-resolution accelerometers have been used to  
147 detect prey capture attempts by SES (Guinet *et al.* 2014, Jouma'a *et al.* 2016), providing  
148 critical insight into interactions between these top predators and the MTLs. Importantly, this  
149 approach has opened the possibility of indirectly mapping the distribution of mesopelagic  
150 prey targeted by SES, in particular myctophid fish (Cherel *et al.* 2008, Vacquié-Garcia *et al.*  
151 2015). While more detailed information on MTL prey encountered by northern elephant seals  
152 has been collected by camera tags (Naito *et al.* 2013), the high energy consumption of these  
153 devices has limited the amount of data that can be collected (Watanabe and Takahashi 2013).  
154 More recently, measurements of bioluminescence from some SES prey (Vacquié-Garcia *et al.*  
155 2017, Goulet *et al.* 2020) have provided a means to distinguish classes of prey and their  
156 distribution. However, although these biologging approaches provide insight into the specific  
157 MTL prey targeted by SES (Yoshino *et al.* 2020), they offer little general information about  
158 the distribution of other MTL organisms. New perspectives are now offered by the miniature

159 animal-attached echosounder used in our study. This sonar tag was deployed on female SES  
160 to study mesopelagic predator-prey interactions (Goulet *et al.* 2019). It can detect echoes from  
161 small organisms (ranging from a few millimetres to tens of centimetres) over a short distance  
162 (up to 6 m) in front of the seal, resulting in detailed profiles of sonar backscatter as the animal  
163 dives. Here, we use data recorded by the tag on two SES females to assess the biological  
164 conditions as they forage in contrasting oceanographic regimes off Patagonia (Argentina) and  
165 the Kerguelen Islands. The goal of this study is to assess whether hydroacoustic data collected  
166 from deep-diving SES can contribute to understanding pelagic ecosystems in the SO by: 1)  
167 measuring the variation of MTL abundance and acoustic size within the water column; 2)  
168 documenting the diel vertical migration of MTLs; and 3) mapping spatial variations in MTL  
169 abundance and behaviour, and their relationships to local oceanographic conditions. While the  
170 aim of the present study is not to quantify carbon fluxes, which is beyond the scope of this  
171 paper and not possible at present, it can provide qualitative information on some processes  
172 that are involved in controlling these fluxes.

173

## 174 **Material and methods**

### 175 1. Study sites and logger deployments

176 In October 2018, adult female SES breeding at Peninsula Valdes (Argentina, 42°57'S,  
177 63°59W, abbreviated to PV) and on the Kerguelen Islands (49°21'S, 70°13'E, abbreviated to  
178 KER) were fitted with biologgers using a standard procedure (McMahon *et al.* 2008). The  
179 animals were captured and anaesthetised with an injection of Zoletil100 (1:1 mix of tiletamine  
180 and zolazepam). In each study location, three biologging devices were glued to the animal's  
181 fur using quick-setting epoxy (Araldite AW 1201): a head-mounted sonar tag (Goulet *et al.*  
182 2019), a back-mounted Satellite Relayed Data Logger (CTD-SRDL, Sea Mammal Research



183 Unit, St Andrews, UK), and an ARGOS transmitting tag (SPOT, Wildlife Computers, USA).  
184 The CTD-SRDL recorded conductivity, temperature, and pressure at 1 Hz while also sending  
185 summary data via ARGOS messages. The SPOT tag was included to facilitate recovery of the  
186 tags when animals returned to land, in case the CTD-SDRL had stopped transmitting. At-sea  
187 movements were monitored using the ARGOS satellite-tracking system, and the loggers were  
188 recovered as soon as the seals hauled out for moulting. The three loggers had a total mass of  
189 under 800 g, representing less than 0.5% of the animal weight, and should therefore have  
190 minimal impact on the survival or foraging success of equipped animals (McMahon *et al.*  
191 2008).

192 The sonar tag recorded high-resolution sonar, location, and movement data. GPS positions  
193 were obtained at each surfacing. Pressure and triaxial magnetometer data were recorded at a  
194 sampling rate of 50 Hz while triaxial acceleration was recorded at 200 Hz. The active sonar  
195 had a centre frequency of 1.5 MHz and emitted 10  $\mu$ s pings at a rate of either 12.5 (PV) or 25  
196 (KER) pings per second, with a source level of approximately 187 dB re 1  $\mu$ Pa at 1 m  
197 (Goulet *et al.* 2019). Sound was transmitted and received via a transducer with a -3 dB  
198 beamwidth of approximately 3.4 degrees. The complex returning signal was demodulated and  
199 the resulting baseband signal was sampled at 192 kHz for intervals of 8 ms following each  
200 ping, giving a spatial resolution of about 3.9 mm and a maximum range of 6 m (see Goulet *et*  
201 *al.* 2019 for device specifications). The sonar transducer on the tag has a rigid backing which  
202 does not compress with depth. Therefore, we assume that the performance of the transducer  
203 remains reasonably constant over the depth range explored by SES. More in-depth validation  
204 approaches are still in progress and will be the subject of future papers

205 In order to extend the recording duration, the sonar was switched on and off on a regular basis  
206 with a cycle of 5.5 h on and 5.5 h off for Kerguelen and 24 h on and 24 h off in Argentina.  
207 Both protocols provided a homogenous sampling of all periods of the day throughout the

208 recording duration. The sonar was activated at depths deeper than 50 m for Kerguelen and 15  
209 m for Argentina. The CTD and sonar tags were synchronised by matching the depth data  
210 sampled by their respective pressure sensors following Le Bras *et al.* (2016).

## 211 2. Sonar data processing and analysis

212 The echo level was calculated by first removing the mean values of the in-phase and  
213 quadrature received signals, and then computed as the root-mean square of these two signals.  
214 Echogram images were constructed from the log of the echo level, with each pixel  
215 representing a sonar sample (i.e. 1/192000 s or 3.9 mm of round-trip travel). Similar to  
216 echograms obtained from traditional fishery echosounders, the vertical dimension of the  
217 echogram represents the range to targets while the horizontal dimension represents successive  
218 pings (Figure 1). Hereafter, any insonified object giving an echo will be referred to as a  
219 scatterer, regardless of its nature or size. From the echograms, the two following metrics were  
220 derived:

### 221 *Scatterer count*

222 The scatterer count is the number of pixels for which the echo level exceeds a threshold  
223 chosen to differentiate actual scatterers from background noise. For each sonar-on phase  
224 of the sonar data, the background noise level was calculated from the signal contained in  
225 the last meter of the sonar range. A visual inspection of the sonar data indicated that  
226 targets were rarely evident at this range due to high spreading and absorption losses. The  
227 echo level of all pixels in the ~4.6-5.6 m range were therefore fit to a Rayleigh  
228 distribution to characterise the noise floor, and the detection threshold was set to the 99.9  
229 percentile of this distribution (Figure 2, Supplementary Information). The scatterer  
230 number (SN) was then calculated as the total number of pixels above the detection  
231 threshold for each sonar ping, averaged over a 2-second window, resulting in a proxy for

232 absolute particle abundance. Scatterer abundance was then calculated as the standardised  
233 SN divided by the nominal sampled volume, resulting in an approximate scatterer  
234 abundance value, i.e. number per m<sup>3</sup>. The sample volume was taken as the truncated cone  
235 of the sonar beam in the 1-1.5 m range assuming a 3.4° beamwidth.

#### 236 *Maximum apparent target size*

237 Acoustic studies often use the echo level as a proxy of the target size. In this study, it is  
238 not possible to ascertain the position of small echoic targets in relation to the beam axis,  
239 meaning that the echo level is dependent on the location, with the echo strength of a given  
240 target decreasing as its position departs from the centre of the beam, and varying with the  
241 orientation of the targets as well as their size and composition. However, the high spatial  
242 resolution of the sonar data allowed measurement of the echo duration, which is related to  
243 the target cross-section, shape and composition (Burwen *et al.* 2003). Apparent size was  
244 therefore calculated for each detected scatterer using the duration  $\Delta t$  (s) for which the  
245 echo intensity was above the detection threshold. This was converted to distance to give a  
246 size estimate in metres:  $\Delta t * ss/2 = \text{size}$ , with  $ss$  = sound speed in seawater, taken as a  
247 constant 1500 m/s throughout the record. For each 2-second period, the scatterer with the  
248 largest apparent size was retained as the Maximum Apparent Size (MAS). Although the  
249 smallest organic particle size detectable by the sonar tag is about 1 to 2 mm (L. Petiteau,  
250 personal communication, Supplementary Information, Figure 4), the smallest apparent  
251 size that can be calculated is 3.9 mm due to the limited sonar resolution. This spatial  
252 resolution allows, in theory, the detection of most mesozooplanktonic organisms of high  
253 ecological importance such as calanoids (e.g. *Rhincalanus gigas*), euphausiids (e.g.  
254 *Euphausia vallentini*), hyperiids (e.g. *Themisto gaudichaudii*), gelatinous organisms (e.g.  
255 *Rosacea plicata*). Considering that the sonar tag is able to detect targets as small as 1 mm  
256 (see Supplementary Information), it is also probable that smaller copepods (e.g. *Calanus*

257 *simillimus*, *C. acutus*) contribute to the signal obtained. The apparent size is dependent on  
258 many factors including the distance, orientation and composition of the target, and its  
259 position relative to the beam axis, making this a noisy proxy for the real size. We  
260 therefore graded the MAS into two broad size classes based on the ‘Sieburth-scale’  
261 plankton classes (Sieburth *et al.* 1978): the first class contained small scatterers with MAS  
262 up to 20 mm which we considered as mesoplankton-like objects. The second class  
263 contained objects with MAS ranging from 20 to 50 mm which were considered as small  
264 macroplankton. Objects with MAS larger than 50 mm were rare (representing 2.2% and  
265 2.9% of the signal for PV and KER respectively) and were often associated with a jerk  
266 (i.e. rapidly changing acceleration signal) which most likely indicates a prey capture  
267 attempt (Ydesen *et al.* 2014). These large targets are therefore likely to be macronekton,  
268 including the mesopelagic fish and squids preyed upon by SES (Daneri and Carlini 2002).  
269 This latter size class was therefore removed from the analysis to focus on potentially  
270 zooplanktonic organisms.

271 The above sonar metrics were calculated over non-overlapping 2-second windows and  
272 extracted at distances ranging from 1 to 1.5 m ahead of the elephant seal’s head. The lower  
273 distance limit was chosen to be beyond the sonar near-field and yet close enough to  
274 potentially detect echoes from the full-size range of MTL organisms. The 0.5 m analysis  
275 range was a trade-off between a narrower range, which may lead to too few detections for  
276 statistical evaluation, and a larger sampling range over which the probability of detection  
277 would vary substantially and hence complicate analysis.

278 Combining these acoustic metrics with the depth and GPS positioning collected by the tag  
279 resulted in a set of time-depth profiles similar to the oceanographic data profiles obtained with  
280 CTD loggers deployed on SES (Fedak 2004). The acoustic data were analysed with  
281 MATLAB R2019b, using custom functions.

### 282 3. Water body classification

283 A typology of the water bodies was established to investigate whether scatterer abundance on  
284 the one hand, and day versus night vertical distribution on the other hand, varied according to  
285 the oceanographic conditions encountered by the seal. Despite the good spatial and temporal  
286 resolution of SO fronts position estimation (Sallée *et al.* 2008), finer-scale structures, such as  
287 sub-mesoscale eddies or meanders, can have a strong impact on biological structure at a more  
288 local scale (Chapman *et al.* 2020), and by extension on the foraging behaviour of SES (Della  
289 Penna *et al.* 2015, Siegelman *et al.* 2019). Pauthenet *et al.* (2017) demonstrated that high-  
290 resolution oceanographic data sampled by CTD tags on SES can be used to objectively define  
291 the geographical extents of water bodies by analysing joint variation of temperature (T) and  
292 salinity (S). We therefore produced profiles of temperature and salinity for each dive, and fit  
293 B-splines to the sampled points. The structural variability between the splines was evaluated  
294 using the functional principal component analysis (FPCA) method developed by Ramsay and  
295 Silverman (2005), which is similar to a principal component analysis except that B-spline  
296 coefficients are used instead of raw data. Usage of FPCA enabled us to retain information  
297 about the shape of the temperature and salinity profiles (Nerini and Ghattas 2007, Pauthenet  
298 *et al.* 2017) while also allowing comparison between locations and individuals by smoothing  
299 out irregularities in data sampling.

300 Temperature and salinity profiles were generated on a constant vertical grid from 20 m to 200  
301 m. This depth range was chosen to maximise temporal coverage especially at night when SES  
302 make shallower dives. As the objective of this analysis step was to describe near-surface  
303 mesoscale oceanic features that may influence MTL distribution, information loss on water  
304 structures below 200 m was not critical to our study. Dives shallower than 200 m were  
305 therefore removed. Oceanographic profiles were then decomposed on a B-spline basis with  $c$   
306 coefficients estimated by polynomial regression (see Ramsay and Silverman 2005). The

307 FPCA method was applied to the set of coefficients resulting in a compact representation of  
308 each profile according to its degree of similarity to the first principal components (PCs)  
309 generated by the FPCA.

310 Clusters of similar curves were discriminated using k-means supervised classification. The  
311 classification of temperature and salinity curves was achieved in the space of the 5 first PCs.  
312 These PCs account for more than 90% of the total inertia and 98 % and 91.5% of the entire  
313 variability for KER and PV, respectively. Based on the Ward criterion, minimising the total  
314 within-cluster variance, we determined the number k of clusters for each SES track, with a  
315 maximum of five groups (Murtagh and Legendre 2014). Different clusters were considered as  
316 representing different water bodies and were then projected to their geographical positions  
317 along the track of the elephant seal, and did not necessarily correspond to the water bodies  
318 traditionally identified in these regions by other studies (Carter *et al.* 2008)

#### 319 4. Analysis of vertical distribution

320 Each scatterer sampled by the sonar tag was assigned to a given water body as defined by the  
321 cluster analysis, according to the oceanographic conditions in which they were encountered.  
322 Although SES perform long-range foraging trips, they only travel a few tens of kilometres per  
323 day. This pace allows capturing large-scale phenomena such as mesozooplankton swarms  
324 (Fielding *et al.* 2014), and also the daily DVM, which is relatively consistent in the same  
325 water body (Behrenfeld *et al.* 2019). Migration behaviour, however, is suspected to be  
326 dependent on the organism type, which may lead to a time-varying vertical distribution of  
327 different-sized scatterers. We therefore determined the relative abundance in the water  
328 column of each scatterer size class (i.e. smaller than 20 mm and from 20 to 50 mm) according  
329 to the period of the day. As the prey of SES performed DVM as well, and were shallower at  
330 night, the sampling effort for the lower depths was unbalanced between day and night. The

331 day period was determined using the sun angle for the current position of the seal (Guinet *et*  
332 *al.* 2014). Then, for each water body, the mean abundance of each scatterer class for each 10-  
333 metre depth bin was calculated. The percentage difference between day and night means in  
334 each depth bin was computed to summarise the relative difference in migration behaviour for  
335 the two size classes.

336 The intensity of the DVM, for each water type, was determined by comparing the depth range  
337 of the migration (i.e. vertical amplitude), the total estimated abundance of scatterers present in  
338 the water column, and the mean acoustic size composition over the same depth range. For  
339 each profile, the depth with the highest abundance of scatterers was considered to represent  
340 the depth containing most of the organisms participating in the DVM. For each dive, the  
341 vertical distribution of the scatterers was determined by a simple peak-finding procedure. In  
342 most dives the vertical distribution of abundance was unimodal. In the case of a multimodal  
343 distribution, the largest mode was taken as the depth of maximum abundance. For each  
344 location, the range between the deepest and the shallowest abundance maximum was defined  
345 as the DVM range. Over these DVM ranges, the total abundance of scatterers was estimated  
346 by adding up interpolated values of the abundance for each depth meter. Finally, the mean  
347 size of the scatterers over the same depth ranges was compared between day and night in each  
348 water body. The numbers of samples for the different possible combinations of analysis  
349 categories (i.e. day period and water body) were unbalanced and heteroscedastic. Therefore,  
350 analyses assessing the effect of the period of the day and the water body were conducted  
351 using a multiway rank-based analysis (Rfit, Kloeke and McKean 2012). Considering the large  
352 oceanographic differences between KER and PV regions, analyses were performed separately  
353 for each location, to compare DVM range, total abundance and size composition. Analyses  
354 were carried out with R software (R 3.5 R core team 2019).

355

356 **Results**

357 1. Sonar observations

358 The maximum depth and mean ( $\pm$  standard deviation) diving depths were respectively 936 m  
359 and  $413 \pm 136$  m for KER individual with a mean diving depth of  $321 \pm 109$  m at night and  
360  $499 \pm 105$  m during the day, and 1109 m and  $392 \pm 249$  m for PV individual with a mean  
361 diving depth of  $218 \pm 108$  m at night and  $539 \pm 272$  m during the day. A total of 313.8 and  
362 408.8 hours of sonar data for KER and PV, respectively, were analysed. The abundance of  
363 scatterers ranged from 7 to 11940 scatterers.m<sup>-3</sup> in KER (mean =  $490 \pm 530$  and from 13 to  
364 13800 scatterers.m<sup>-3</sup> in PV (mean =  $795 \pm 1465$ ). The echo signal was dominated by small  
365 objects ( $< 20$  mm), representing 52.4% of scatterers in KER and 93.9% in PV, whereas the  
366 20-50 mm size class represented 44.7% and 5.6% of the objects detected in KER and PV  
367 respectively.

368

369 The signals recorded by the sonar tag showed wide variability with time and depth (Figures 2  
370 and 3). Scatterer abundance was the highest in the upper 200 m of the water column in both  
371 regions, for both day and night.

372 A portion of the KER recording (Nov 11<sup>th</sup>-15<sup>th</sup>, Figure 2) showed an unusually high  
373 abundance of scatterers throughout the entire water column (from 70 m to 500 m) (Figures 1.b  
374 & 1.c). Over these 4 days, the mean size of the scatterers was  $12 \pm 4.5$  mm.

375

376 A DVM pattern appeared to be the main driver of the vertical heterogeneity of the PV sonar  
377 signal data, in terms of scatterer abundance (Figures 3 and 5). This feature was not as clear for  
378 the KER dataset (Figures 2 and 4).



379

380 2. Classification of water bodies and scatterer size differences

381 A total of 2094 and 2819 dives for KER and PV, respectively, were used for the FPCA  
382 procedure (representing 96.9% and 85.5% of the available profiles; the remaining profiles did  
383 not reach 200 m).

384 The first two principal components (PC) accounted for 80.1% and 89% of the variability in  
385 the individual profiles for PV and KER, respectively. CTD profiles were distributed within  
386 three water clusters for PV, with 226, 1819, and 364 profiles recorded for water clusters 1, 2,  
387 and 3, respectively. The water bodies were distributed along both temperature and salinity  
388 gradients, with, for each location, colder and less salty waters for cluster 1 and warmer and  
389 saltier waters for cluster 3 (Figure 6).

390 3. Analyses of vertical distribution

391 When considering all scatterers regardless of size, the mean vertical extent of the abundance  
392 maximum ranged from 30 to 260 m in PV (Figure 7) while a narrower depth range from 70 m  
393 (i.e. the turn-on depth of the sonar) to 160 m was observed at KER (Figure 8).

394 For KER, there was a significant difference in the depth of peak abundance between day and  
395 night ( $p$ -value  $> 0.001$ ), but no significant variation in depth between clusters (Figure 8).

396 However, significant differences in scatterer abundance were found between water clusters  
397 ( $p$ -value  $< 0.005$ ). The mean size of scatterers differed significantly across water clusters, but  
398 no diel differences in this parameter were observed. Larger scatterer sizes were encountered  
399 in water clusters 1 ( $14.7 \pm 5$  mm) and 2 ( $14.8 \pm 3.7$  mm) compared to water cluster 3 ( $11.8 \pm$   
400  $3.8$  mm) ( $p$ -value  $< 0.001$ ).

401 For PV, due to the 24-hour duty-cycle, no sonar profile was available for the night period of  
402 water cluster 1. For daylight hours, the depth of the main abundance peak differed  
403 significantly between the 3 water clusters (p-value < 0.001), with a deeper location in water  
404 clusters 2 and 3 compared to water cluster 1 (p-value < 0.001). Furthermore, the depth of the  
405 abundance maximum was significantly deeper during the day than the night for water clusters  
406 2 and 3 (day:  $113 \pm 56.5$  m, night:  $42.3 \pm 18.9$  m, p-value < 0.001, for water cluster 2; day:  
407  $126 \pm 49$  m, night:  $40.1 \pm 13.1$  m, p-value < 0.001 for water cluster 3; Figure 7b). The total  
408 number of scatterers, totalled over the depth range 30:260 m, was also significantly different  
409 between day and night for these water clusters (day:  $194.10^3 \pm 48.10^3$ , night  $185.10^3 \pm 52.10^3$   
410 for water cluster 2; day:  $250.10^3 \pm 68.10^3$ , night  $125.10^3 \pm 46.10^3$  scatterers.m<sup>-3</sup>, for water  
411 cluster 3, Figure 7c), but did not differ significantly between them. However, significant  
412 differences in scatterer size were found between the three clusters during the day (p-value >  
413 0.001) when they could be compared (water cluster 1:  $15.4 \pm 6.6$  mm, water cluster2:  $10.7 \pm$   
414  $5.4$  mm, water cluster 3:  $11.5 \pm 5.4$  mm, Figure 7d).

415 The percentage difference between day and night for each scatterer size class in 10-metre  
416 depth bins showed a regular pattern of maximum abundance in upper layers at night, and in  
417 lower layers during the day (Figure 9). Depending on the water body, small (i.e. < 20 mm)  
418 and medium-sized (20-50 mm) scatterers exhibited some differences in their vertical  
419 distribution patterns (Figure 9).

420 Finally, clear differences were evident between KER and PV when looking at the complete  
421 depth range of 70 to 260 m that was sampled during the two surveys. Although the average  
422 scatterer abundance was similar in the two locations, PV data exhibited greater differences  
423 between the day and night vertical distributions of scatterers (p-value < 0.001, Figure 10a).  
424 However, the mean size of scatterers was greater for KER ( $25.1 \pm 7.1$  mm, max = 175 mm)  
425 compared to PV data ( $17.4 \pm 6.2$  mm, p-value < 0.05, max = 351 mm, Figure 10b).

426

## 427 **Discussion**

### 428 1. Horizontal and vertical heterogeneity in the acoustic backscatter

429 Two sonar tags were deployed in parallel on elephant seals from distinct oceanographic  
430 regions to assess their performance in capturing the sizes, vertical distribution and diel  
431 dynamics of MTL organisms. While a previous study showed that mesopelagic fish/squids  
432 were detected by the sonar tag during close prey encounters (Goulet *et al.* 2019), the present  
433 study quantifies the abundance of smaller acoustic targets, insonified by the tags as the seals  
434 dived through the water column. The primary aim of this study, presenting the first-ever  
435 application of the new biologger, is therefore to assess its potential for quantifying the vertical  
436 and horizontal distribution of the MTLs during the far-ranging foraging trips of SES.

437 It is important to note that using a free-ranging foraging animal as a sampling platform may  
438 ineluctably lead to some sampling bias. Foraging SES tend to target, and therefore  
439 oversample, highly dynamic areas such as fronts (Cotté *et al.* 2015, Della Penna *et al.* 2015,  
440 Rivière *et al.* 2019) characterised by complex hydrodynamic conditions, which are favourable  
441 for prey aggregation. In contrast, SES may tend to undersample areas of lower organism  
442 concentrations. However, this prey bias was reduced in this study by excluding portions of the  
443 sonar signal corresponding to prey catch attempts. As a result, only MTL organisms which  
444 were not targeted by the SES were investigated in the present study. Conversely, it should  
445 also be noted that some of the sampling biases associated with the use of non-biological  
446 platforms, such as gliders or Argo floats, are absent when using animal platforms. For  
447 example, Haëntjens *et al.* (2020) report a possible attraction of MTL organisms to the LEDs  
448 used on Argo floats, which is avoided by the sonar tag without LEDs. In addition, the slow

449 descent speed of a float is likely to cause a gathering of organisms in the echosounder beam,  
450 whereas the vertical speed of the elephant seal of about 1.4 m/s prevents any flock formation.

451 A comparison between an underwater vision profiler and a sonar tag for measuring organism  
452 abundance has revealed the sonar tag's ability to detect organisms as small as 1 mm in  
453 diameter (unpublished data; Petiteau in prep., Supplementary Information). However, it is  
454 important to underline that the method used in this study cannot distinguish between several  
455 small, closely aggregated targets (i.e. separated by less than 3.9 mm, the spatial resolution of  
456 the sonar), and a single target of the same apparent size. Nevertheless, as the deep-water  
457 environments visited by foraging SES contain relatively few particles, the first scenario is  
458 rarely encountered, and should contribute only slightly to overall abundance estimates. Given  
459 the potential range of backscatter sources, the sonar tag data from SES in KER and PV likely  
460 include backscatter from a combination of objects whose nature cannot be determined,  
461 whether biological debris passively sinking to the ocean floor, or living organisms, some of  
462 them undertaking diel vertical migrations.

463 The main limitations being stated, we found that scatterers were more abundant and produced  
464 higher-intensity echoes in the upper part of the water column (i.e. above 250 m deep) in both  
465 locations. Temporal variations of the backscatter distribution were consistent with a daily  
466 cyclic movement in the water column corresponding to the daily migration of MTL  
467 organisms. However, this diel signal was not evident continuously throughout the datasets,  
468 and so is likely dependent on the nature of the scatterers present locally. Specifically, when  
469 the backscatter is dominated by small-size non-migrating items, we suggest that this could be  
470 indicative of biological detritus or else small-size non-vertically-migrating zooplankton, such  
471 as *Calanus propinquus* (Conroy *et al.* 2020), highly abundant in the eastern sector of the  
472 Kerguelen shelf (Carlotti *et al.* 2008).

473 We also found evidence that both the horizontal and vertical distributions of scatterers vary  
474 according to the oceanographic conditions encountered. Five distinct water bodies were  
475 identified along the seal tracks, corresponding closely with weekly estimates of SO fronts  
476 positions (Sallée *et al.* 2008). Only one of these water bodies, water body 3, corresponding to  
477 Sub-Antarctic Waters (SAW), was encountered by seals from both KER and PV. Each seal  
478 also encountered two other water types but these were distinct in each location.

479 For the PV seal, clear differences in the vertical distribution, abundance and size of scatterers  
480 were found between each oceanographic domain visited, evidencing a change in MTL  
481 community composition and/or abundance depending on the water body. The changes in  
482 water body along the track may indicate that the seal encountered sub-mesoscale  
483 oceanographic features. Such structures are frequently used by SES and are often linked with  
484 improved foraging conditions (Dragon *et al.* 2010, Della Penna *et al.* 2015, Siegelman *et al.*  
485 2019). Currently, the datasets are too limited to investigate the commonalities and differences  
486 of scatterers among similar water bodies, or to investigate seasonal changes. We can  
487 nevertheless expect an increased number of deployments of this tag, and the large ranges  
488 covered by SES, to lead to studies comparing the different large-scale water bodies explored  
489 by SES.

## 490 2. Regional differences in sonar signal

491 In both study areas, the abundance of scatterers varied depending on the water body. For the  
492 PV seal, significantly higher scatterer abundance was found in water body 1, which was close  
493 to the continental shelf, compared to the two other water bodies it encountered. This might be  
494 related to the highly productive waters of the Patagonian continental shelf, which receive  
495 nutrient-enriched inputs from the Malvinas current and support a large spring bloom (Lutz *et*  
496 *al.* 2018) with likely enhanced secondary production (Cepeda *et al.* 2018). However, the prey

497 catch rate of the seal is low within this water body compared to elsewhere along its track,  
498 suggesting that this high spring productivity may not lead to increased abundance of the prey  
499 targeted by SES, or with a delay, due to the temporal decoupling of primary producers and  
500 primary consumers (Latasa *et al.* 2014). Further offshore, within the Sub-Antarctic Front  
501 (SAF) northward inclusion, primary production tends to be lower and supports communities  
502 of small mesozooplankton with lower biomass (Thompson *et al.* 2013) — a tendency that  
503 appears to be supported by the sonar tag data, revealing fewer and smaller scatterers with a  
504 very clear DVM pattern.

505 Similarly, MTL abundance in KER differs according to water mass, with the lowest  
506 abundance observed for water body 3 and the highest for water body 1. Water body 3  
507 comprises profiles in the area around the North SAF and can be considered as a different  
508 bioregion than the other water bodies influenced by the subtropical regime (Godet *et al.*  
509 2020). The warmer waters of this region tend to be associated with lower chlorophyll-*a*  
510 concentration and overall lower productivity than the high-productivity shelf and off-shelf  
511 waters of the Kerguelen plateau (Godet *et al.* 2020). The high abundance of scatterers seen in  
512 water body 1 may be associated with these enriched plateau waters, with eastward advection  
513 by currents releasing soluble iron, and enhancing primary production (Robinson *et al.* 2016,  
514 Schallenberg *et al.* 2018).

515 Overall, a higher abundance of larger-sized scatterers was encountered in KER compared to  
516 PV waters while the DVM pattern is more obvious within the PV dataset. These findings  
517 exemplify the differences between these two distinct marine provinces (Longhurst 2010, Fay  
518 and McKinley 2014). Our results also highlight the wide variability in vertical distribution  
519 patterns of the MTLs, a finding consistent with recent fine-resolution studies (Pinti and Visser  
520 2018, Conroy *et al.* 2020) and global ocean studies (Behrenfeld *et al.* 2019). More extensive

521 deployments of the sonar tag may therefore help improve our understanding of the  
522 environmental and biological factors that drive these differences.

### 523 3. Diel vertical migration

524 The current study also reveals fundamental differences in the vertical distribution and  
525 behaviour of zooplanktonic and micronektonic organisms according to their sizes. A day-  
526 scale cyclic vertical movement of a portion of the scatterers was evident in sections of the  
527 sonar recordings (see Figures 4.b & 5.b) comprising an upward migration at dusk and a  
528 downward one at dawn. The presence of this diel pattern in our data confirms the ability of  
529 the sonar tag to detect mesopelagic organisms, such as macrozooplankton, or other small  
530 MTL organisms involved in the DVM.

531 The extent of the vertical migration recorded by the sonar tag in both regions, reaching 160 m  
532 deep in KER and 260 m deep in PV, does not match the migration range of mesopelagic fish  
533 such as myctophids, and squid (Davison *et al.* 2015, Bianchi and Mislán 2016, Béhagle *et al.*  
534 2016, Kloser *et al.* 2016), which is also revealed by the day and night mean diving depth of  
535 the two seals. Therefore, the observed DVM likely represents the vertical movement of  
536 zooplankton (i.e. the prey of SES prey) although inferences about the size of scatterers from  
537 the sonar data require validation. However, the minimum spatial resolution of the sonar tag  
538 (approx. 3.9 mm) means that smaller organisms will be lumped within the smallest size class  
539 resolved by the sonar tag. Nonetheless, the mean acoustic size (2 to 3 cm) of the migrating  
540 scatterers, and the depth range at which they are detected, suggest large zooplanktonic  
541 organisms like euphausiids. Indeed, the Kerguelen waters host high abundances of euphausiids  
542 (Cuzin-Roudy *et al.* 2014, Koubbi *et al.* 2016, Godet *et al.* 2020) such as *Thysanoessa*  
543 *macrura* and *Euphausia vallentini*, both with an adult size close to 3 cm. The Argentinian  
544 Patagonian waters also host high densities of *E. vallentini* (Cepeda *et al.* 2018). This krill

545 species makes a diel migration between 100 and 250 m depth (Cuzin-Roudy *et al.* 2014),  
546 matching the vertical range of the migration detected by the sonar tag in this location.

#### 547 4. A possible marine snow event recorded off Kerguelen

548 Between November 10<sup>th</sup> and 14<sup>th</sup>, the sonar tag deployed in KER recorded anomalously high  
549 and constant scatterer abundances throughout the epipelagic layer to 500 m deep. This could  
550 have been caused by large concentrations of salps (Wiebe *et al.* 2010), and validation of the  
551 sonar tag is required to determine the typical echo signals generated by low-target strength  
552 targets such as salps and jellyfish. However, the homogeneous distribution along the vertical  
553 dimension could also indicate a mass sinking event of biological detritus, known as marine  
554 snow (Aldredge and Silver 1988, Turner 2015). Marine snow events follow periods of high  
555 productivity, when heavy phytoplankton cells and zooplankton faecal pellets sink downwards  
556 rapidly (Laurenceau-Cornec *et al.* 2015b). Some studies suggest that these events, occurring  
557 off the Kerguelen plateau twice a year during the seasonal blooms, represent, in the SO, one  
558 of the main contributions to the biological pump that exports particulate organic carbon  
559 (POC) to depth (Turner 2015, Rembauville *et al.* 2015). The spatial co-occurrence between  
560 such events and satellite-assessed POC from remote sensing may help resolve this question in  
561 the future (Tran *et al.* 2019).

#### 562 5. Where is the Deep Scattering Layer?

563 A vast majority of the scatterers recorded by the sonar tags come from the epipelagic zone,  
564 whereas beneath 300 m, in the mesopelagic layer, echoes were scarce. One of the most  
565 notable acoustic features of the global ocean, the deep scattering layer (DSL), is therefore not  
566 immediately evident in the sonar tag data. The DSL, mainly composed of mesopelagic fish  
567 and squids (i.e. the main prey of SES), is found in the mesopelagic zone at a depth of around  
568 400 to 500 m throughout the world oceans (Proud *et al.* 2018), and particularly in the SO



569 (Kloser *et al.* 2016, Béhagle *et al.* 2017). This depth is consistent with the mean diving depth  
570 of the SES, and the sonar tag's inability to detect the DSL as a clear pattern in the way that  
571 ship-based echosounders have been found to do, can possibly be explained by their different  
572 sampling resolutions. Ship echosounders are mainly designed to detect mesopelagic scatterers  
573 composed of organisms exceeding several centimetres while the high frequency sonar tag is  
574 well-suited to detect smaller-size organisms. Studies have established that the abundance of  
575 zooplankton and micronekton decreases linearly with size following a log/log function  
576 (Heneghan *et al.* 2016)). Therefore, due to its narrow beam, the water volume sampled by the  
577 sonar tag is limited and may prevent the relatively low densities of micronektonic fish and  
578 squids from being properly assessed. In comparison, ship-based echo-sounders have a larger  
579 beam and are operated from the surface, leading to a much greater insonified volume of water  
580 at greater depths. Such sonars are well suited to sample bulk micronekton but are not so well-  
581 suited to assess small-size and dispersed zooplankton. Therefore, these two approaches should  
582 be seen as complementary with one another. Nonetheless, the bottom phase of SES dives, and  
583 more specifically the depth of prey capture attempts (PCAs), provide a proxy for the DSL  
584 depth in the water column (Guinet *et al.* 2014, McMahon *et al.* 2019). Both the dive depth  
585 and the depth of PCAs, as inferred from acceleration transients recorded by biologging tags  
586 on SES, vary with a diel cycle, presumably tracking the daily vertical migration of  
587 components of the DSL (Figure 4.b and Figure 5.b). The sonar tags frequently recorded  
588 scatterers with a large apparent size simultaneously with PCAs. The focus of the study being  
589 smaller-size MTL organisms, and the time SES spend foraging being disproportionate, PCAs  
590 were excluded from this study. These larger scatterers however likely represent the DSL  
591 organisms targeted by SES and so provide some indication about the density and size  
592 distribution of the DSL that is the topic of a companion paper (Goulet *et al.*, in prep).

## 593 **Conclusion**

594 Although the sonar tag, aided by the persistent diving behaviour of SES, shows considerable  
595 promise for *in situ* studies of the biotic environment of the deep ocean, namely the  
596 distribution and movement of resident organisms, a recurring issue is the lack of certainty in  
597 inferring organism size and type from the echo returns. A key area for future work is therefore  
598 to assess how well the echo patterns associated with different sizes and categories of  
599 organisms can be distinguished with the current tag design. This information is critical for  
600 most trophic and carbon flux studies (Hernández-León *et al.* 2019). While careful tank-based  
601 validation studies can improve confidence in interpreting the sonar tag, ultimately *in situ*  
602 measurements will be most useful for the identification of unique deep-sea fauna that cannot  
603 be held in aquaria. One way to achieve *in situ* validation could be to combine the sonar tag  
604 with a camera tag in such a way that image capture is triggered by acoustic detections within a  
605 given detection range.

606

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## 620 **Declaration of interest:**

621 The authors declare that they have no known competing financial interests or personal  
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623

624

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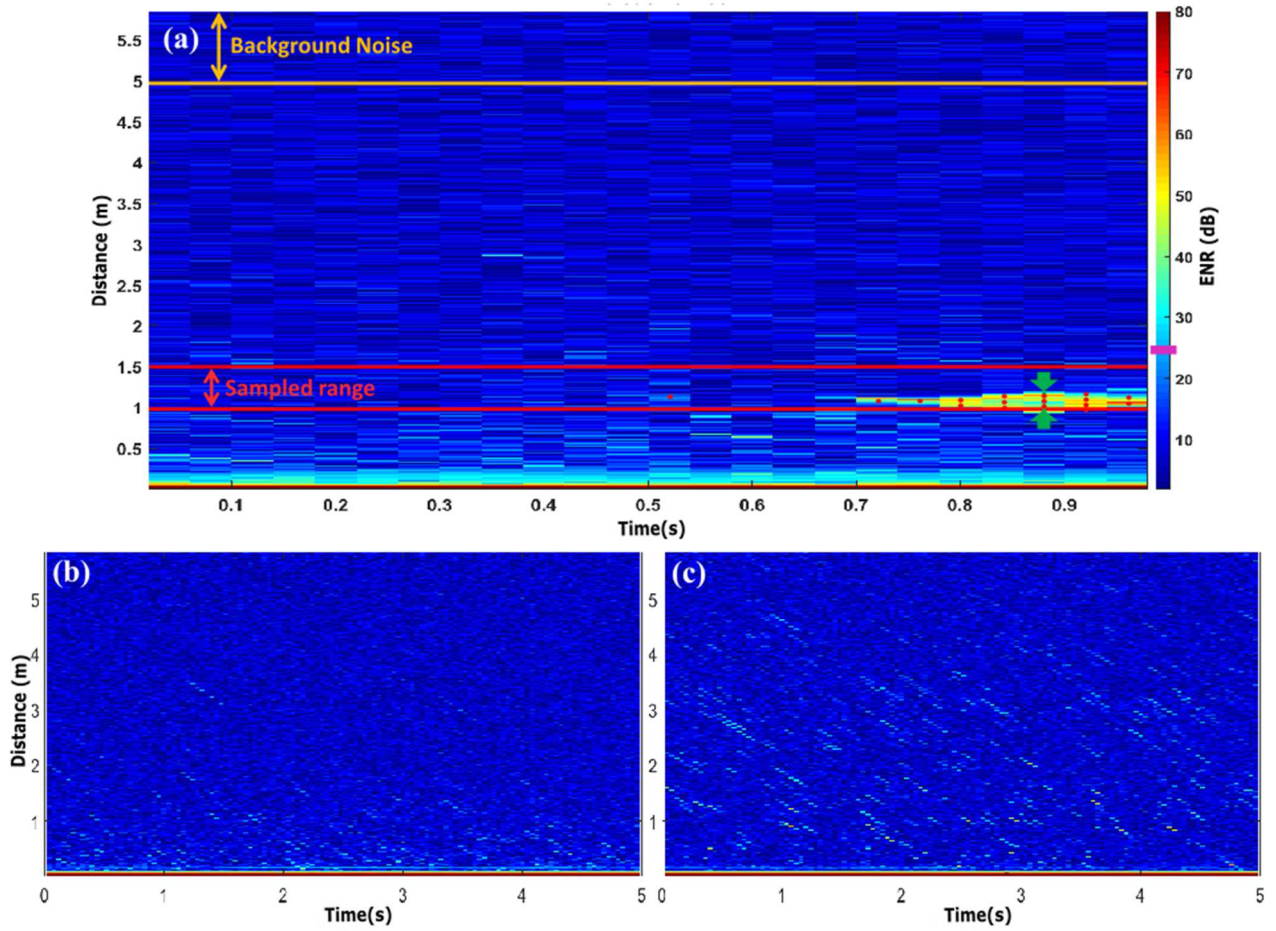
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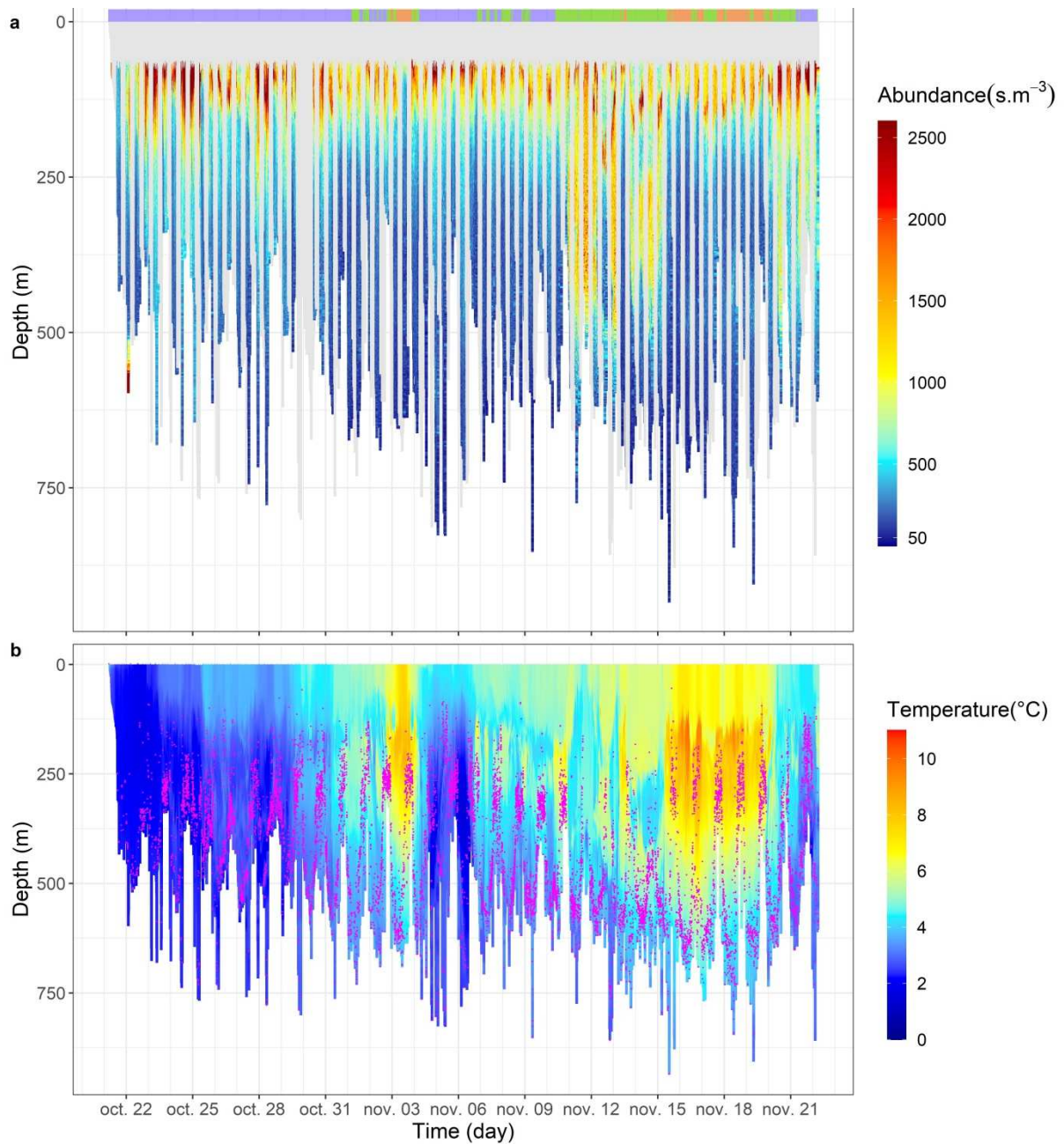
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972 **Figure 1: (a) Echogram with a schematic representation of the metrics calculations. Red lines**  
 973 **mark the analysis range. The orange line shows the range used for Background Noise Level**  
 974 **estimation. (b) Echogram from a regular area. (c) Echogram from the high-intensity signal**  
 975 **region.**

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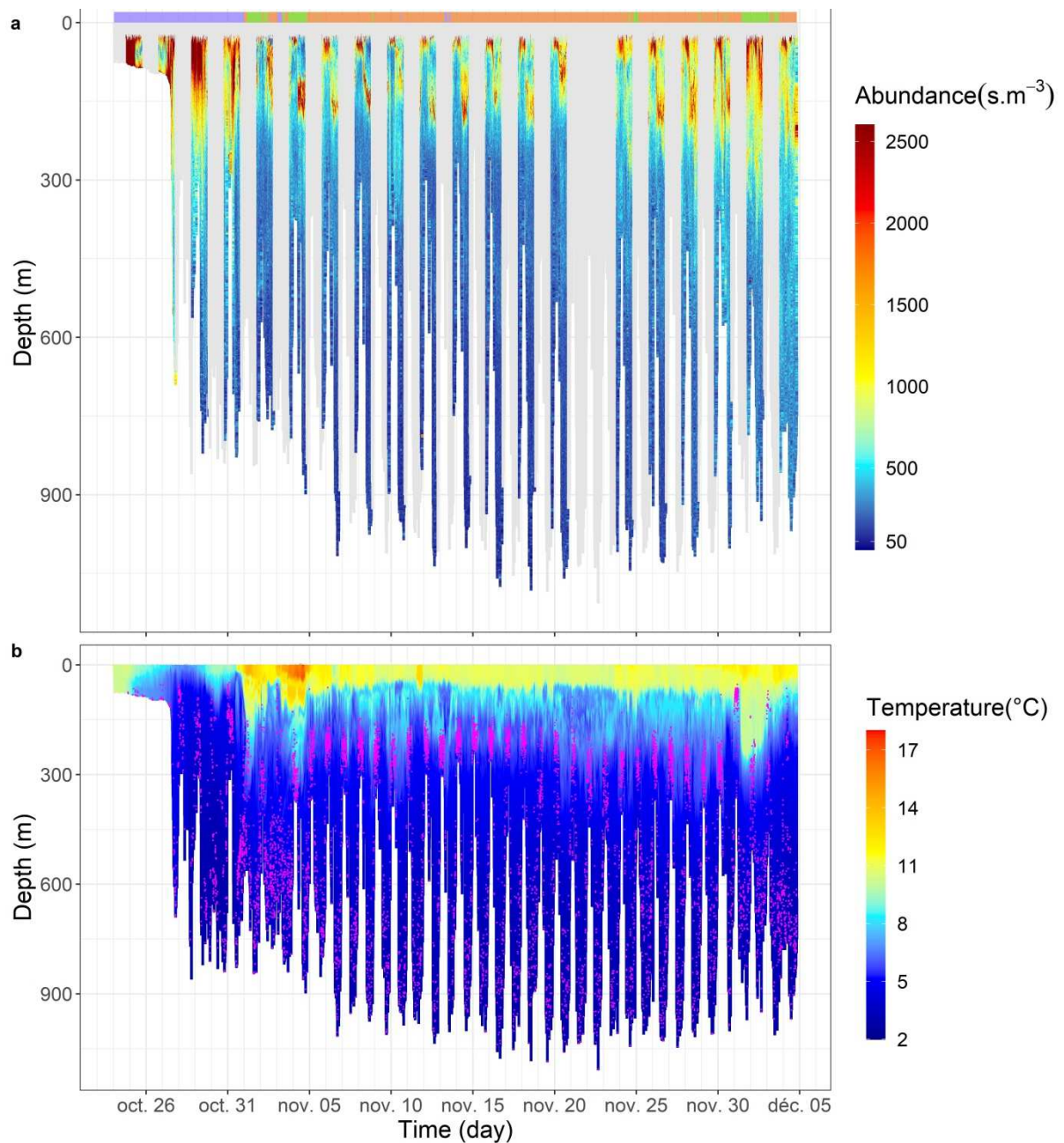


978

979 **Figure 2: (a) Time-depth series of scatterer abundance, expressed in scatterers.m<sup>-3</sup>, detected by**  
980 **the sonar tag on a seal tagged on Kerguelen Island (KER). The coloured rectangles above the**  
981 **plot indicate the position of inferred water body types 1 (purple), 2 (green) and 3 (light orange).**  
982 **(b) Water temperature profiles recorded by a tag on the same animal. Pink points indicate prey**  
983 **capture attempts inferred from acceleration transients.**

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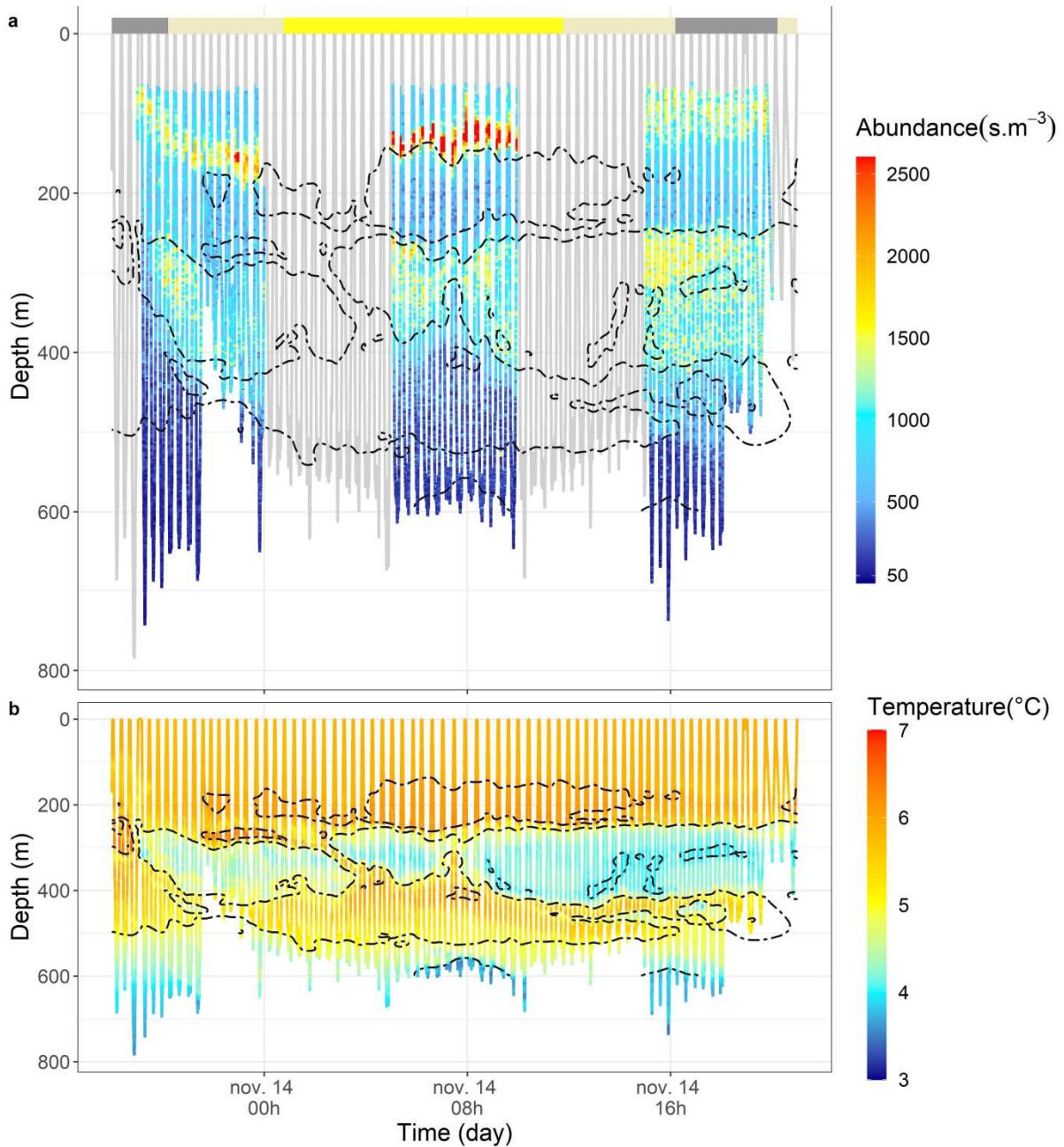
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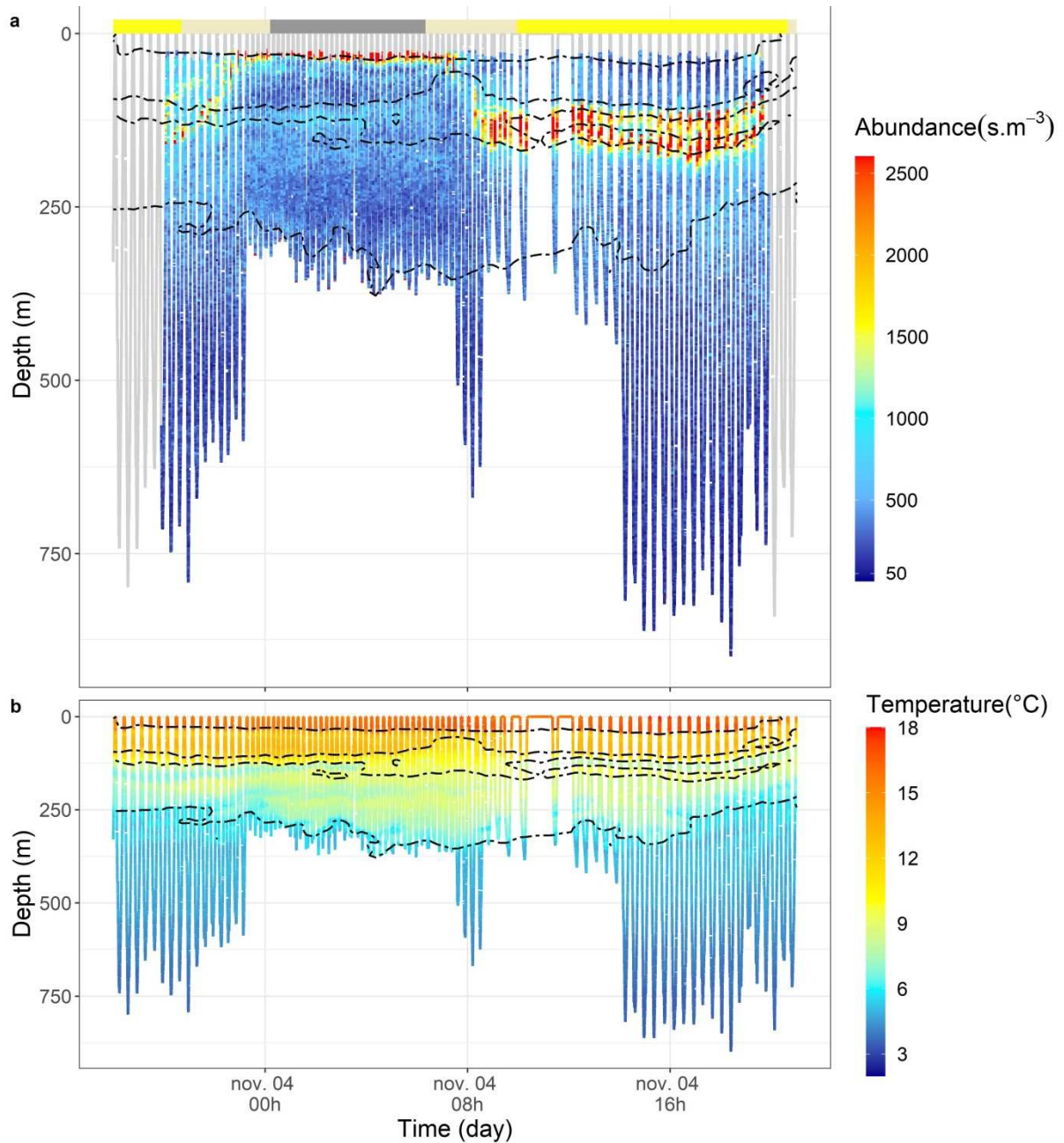
987 **Figure 3: (a) Time-depth series of scatterer abundance, expressed in scatterers.m<sup>-3</sup>, detected by**  
 988 **the sonar tag on a seal tagged on Peninsula Valdes (PV). The coloured rectangles above the plot**  
 989 **indicate the position of inferred water body types 1 (purple), 2 (green) and 3 (light orange). (b)**  
 990 **Water temperature profiles recorded by a tag on the same animal. Pink points indicate prey**  
 991 **capture attempts inferred from acceleration transients. The colour scales have different ranges**  
 992 **than in Figure 2 to accommodate the differing conditions in this oceanographic region.**

993



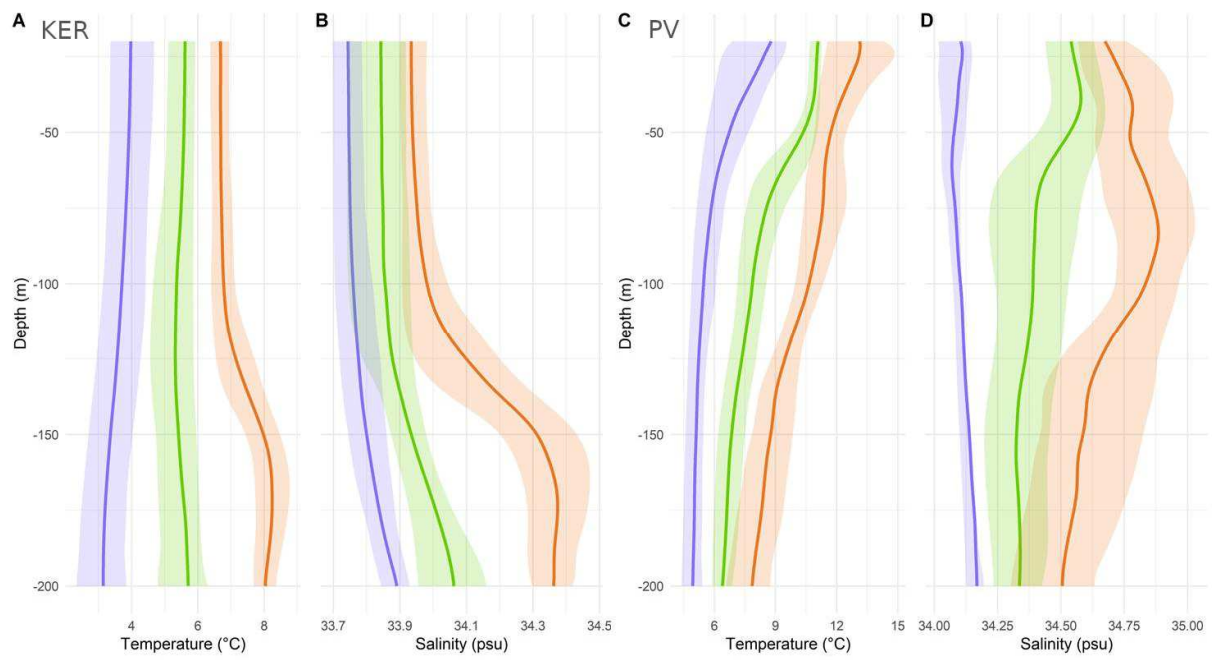
996 **Figure 4: (a) Time-depth representation of the relative abundance of scatterers, expressed in**  
 997 **scatterers.m<sup>-3</sup>, detected by the sonar tag, zoomed over a one-day period for KER. The coloured**  
 998 **rectangles represent the light angle with yellow and grey for day and night, respectively, and the**  
 999 **shaded grey for twilight. The sonar was operated on a 5.5-hour on/off duty-cycle. (b)**  
 1000 **Temperature profiles, in °C for the same time interval. The dotted black lines in both plots**  
 1001 **represent the isotherms, with an increment of 1°C.**

1002



1003

1004 **Figure 5: (a) Time-depth representation of the relative abundance of scatterers, expressed in**  
1005 **scatterers.m<sup>3</sup>, detected by the sonar tag, zoomed over a one-day period for PV. The coloured**  
1006 **rectangles represent the light angle with yellow and grey for day and night, respectively, and the**  
1007 **shaded grey for twilight. The sonar was operated on a 12-hour on/off duty-cycle. (b)**  
1008 **Temperature profiles, in °C for the same time interval. The dotted black line represents the**  
1009 **isotherms, with an increment of 3°C.**

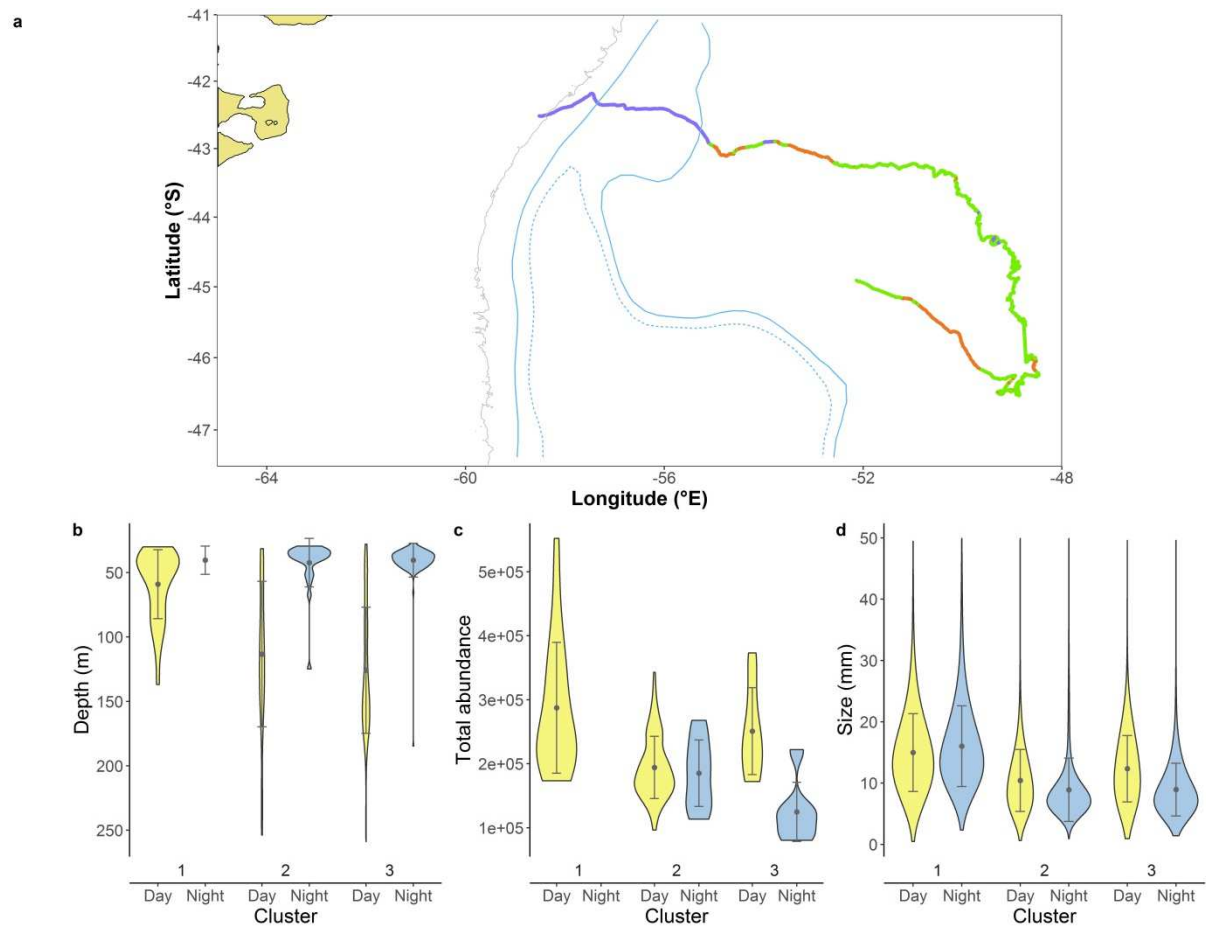


1010

1011 **Figure 6: Average temperature (A, C) and salinity (B, D) profiles of KER and PV datasets. The**  
 1012 **three clusters are shown in blue (cluster 1), green (cluster 2) and orange (cluster 3). For each**  
 1013 **profile, the envelopes are bounded by the first and last quartile and thus contain 50% of the**  
 1014 **profiles.**

1015

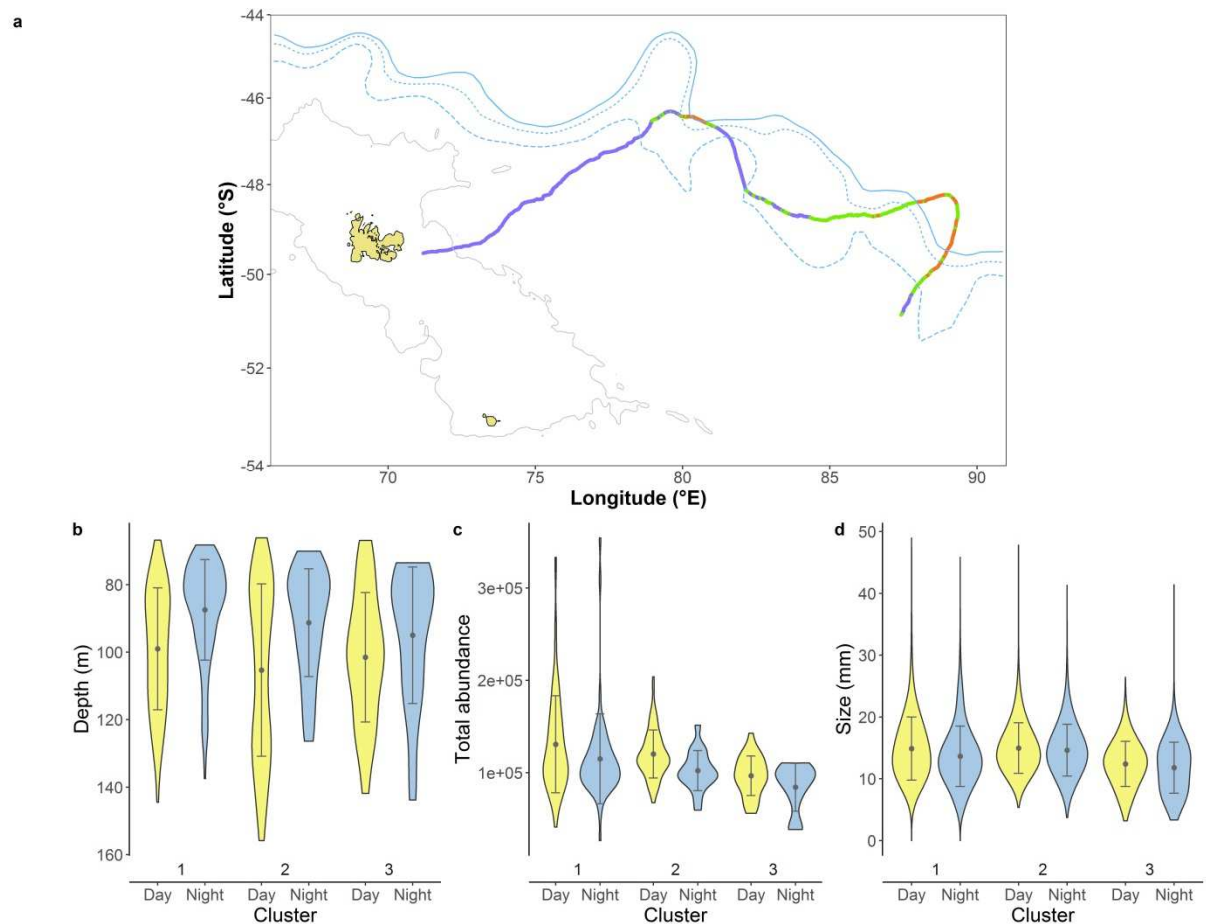
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1017

1018 **Figure 7: (a) Track of the SES tagged on Peninsula Valdés during the interval recorded by the**  
 1019 **sonar tag (FPCA cluster colours as in Figure 6). The solid grey line shows the 1000 m isobath.**  
 1020 **Blue lines indicate the mean position of oceanic fronts over the study period, as given by the**  
 1021 **Centre for Topographic studies of the Ocean and Hydrosphere (see Sallée *et al.* 2008). Lower**  
 1022 **panels: (b) mean day (yellow) and night (blue) DVM depth (maximum abundance of profiles)**  
 1023 **for the 3 water clusters for the PV seal, (c) sum of the scatterers' abundances over the depth**  
 1024 **range 30-260 m (matching the vertical extent of the DVM depth for each cluster), (d) average**  
 1025 **scatterers' size distribution for each cluster. Grey dots and error bars respectively indicate the**  
 1026 **mean of each violin plot and the standard deviation.**

1027

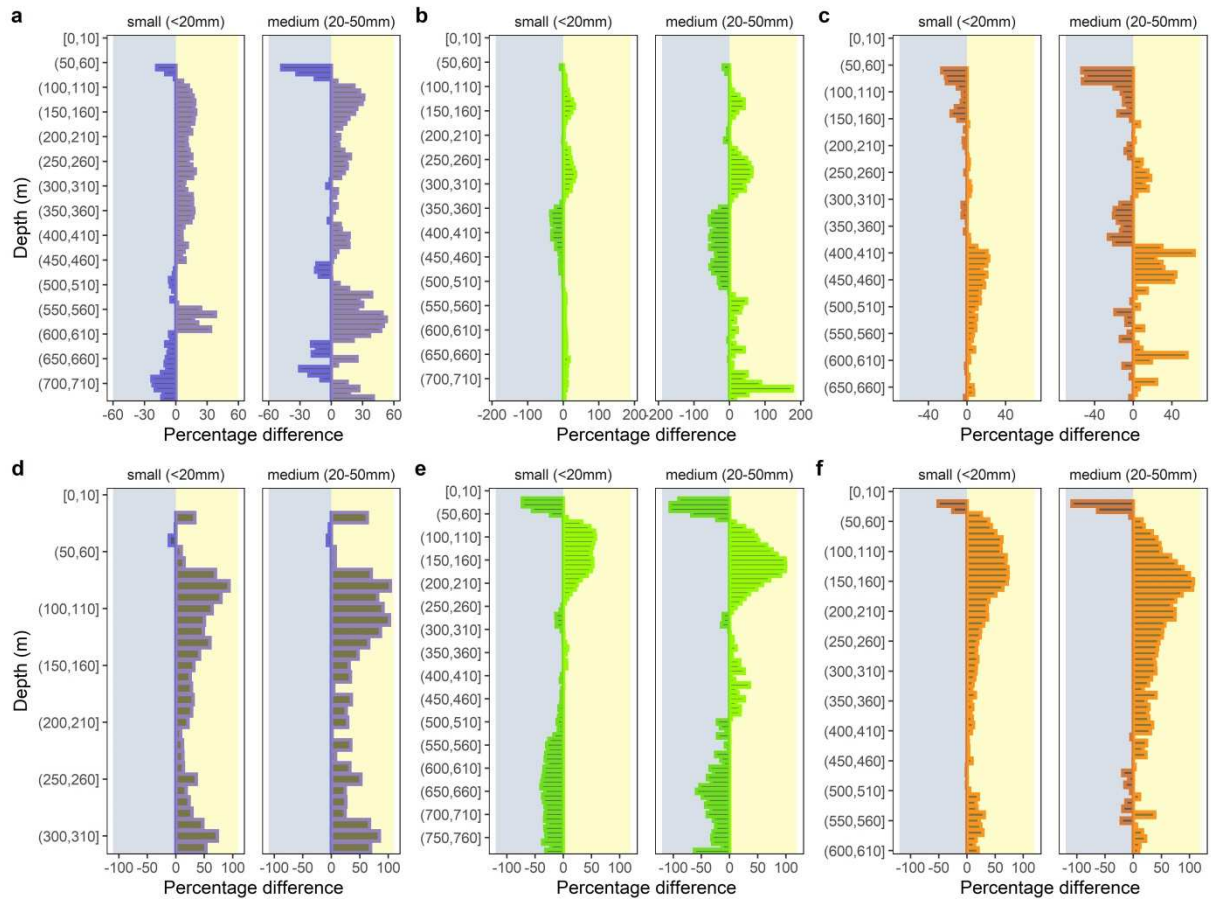


1028

1029 **Figure 8: (a) Track of the SES tagged on Kerguelen Island during the interval recorded by the**  
 1030 **sonar tag (FPCA cluster colours as in Figure 6). The solid grey line shows the 1000 m isobath.**  
 1031 **Blue lines indicate the mean position of oceanic fronts over the study period, as given by the**  
 1032 **Centre for Topographic studies of the Ocean and Hydrosphere (see Sallée *et al.* 2008). Lower**  
 1033 **panels: (b) mean day (yellow) and night (blue) DVM depth (maximum abundance of profiles)**  
 1034 **for the 3 water clusters for the KER seal, (c) sum of the scatterers' abundances over the depth**  
 1035 **range 70-160 m (matching the vertical extent of the DVM depth for each cluster), (d) average**  
 1036 **scatterers' size distribution for each cluster. Grey dots and error bars respectively indicate the**  
 1037 **mean of each violin plot and the standard deviation.**

1038



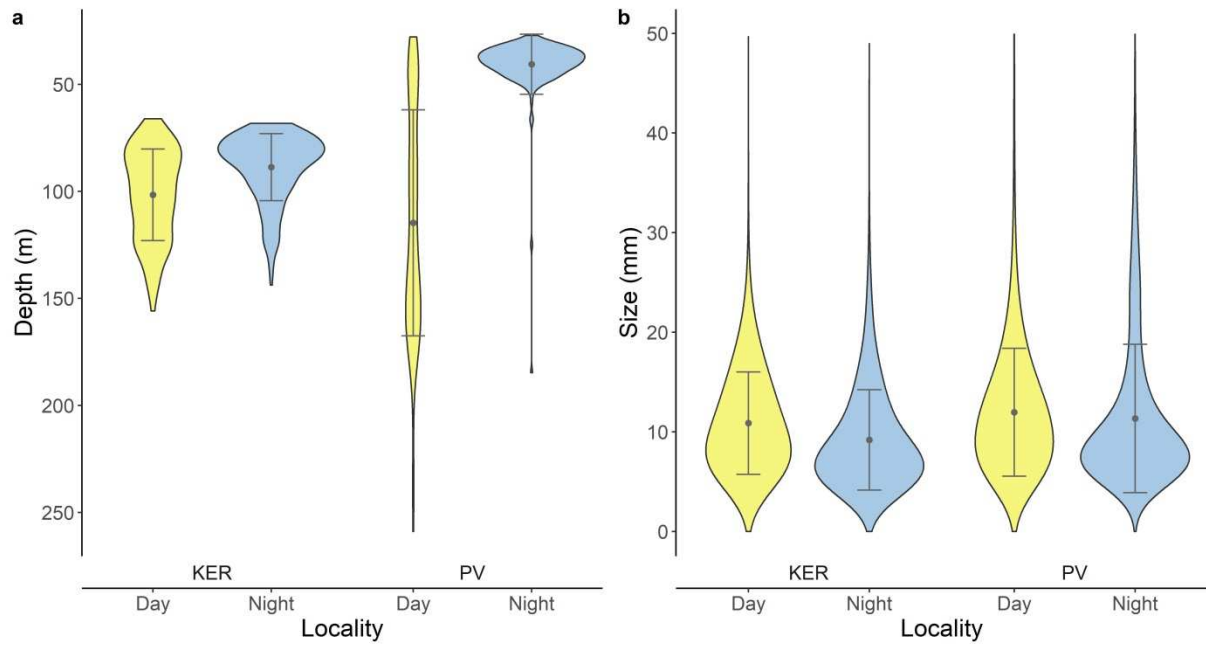


1039

1040 **Figure 9: Percentage difference, for small- (left) and medium- (right) size scatterers between day**  
 1041 **(yellow) and night (grey), calculated over 10-m depth bins, for the three water clusters (colours as**  
 1042 **in Figure 6) for KER (upper panel) and PV (lower panel). Positive values correspond to higher**  
 1043 **abundances during daytime than at night, and conversely a negative difference indicates higher**  
 1044 **abundances at night than during daytime for this depth bin.**

1045

1046



1047

1048 **Figure 10: (a) Mean day (yellow) and night (blue) DVM depth for the 2 locations. The DVM depth is**  
 1049 **the depth with the maximum density over a profile. (b) Mean particle size distribution over**  
 1050 **thedePTH range (70:260). Grey points indicate the mean and the error bars represent +/-1 standard**  
 1051 **deviation.**

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## 1061 **Supplementary information**

### 1062 **Calculation of the sonar tag metrics:**

1063

1064 Intensity threshold definition:

1065 The noise intensity threshold is set on the last meter of the sonar detection range (5 to 6m),  
1066 assuming that the entire signal in this range is ambient noise, and designated as the  
1067 Background Noise Level (BNL).

1068 The amplitude fluctuations in the signal obtained from a shadow area (i.e. area behind a  
1069 target) or from out-of-range detections are essentially electronic noise. The signal amplitude  $X$   
1070 is thus noised with a Gaussian distribution function.

1071 
$$G(X) = \frac{1}{\sqrt{2\pi}\sigma} \exp \frac{-(X - \mu)^2}{2\sigma^2}$$

1072 where  $\mu$  is the mean of the amplitude and  $\sigma$  the standard deviation.

1073 The acoustic signal recorded by the sonar tag is the result of a combination of elementary  
1074 signals, which can be for example caused by a strong scattering phenomenon. For the sonar  
1075 tag, two signal channels of different amplitudes are considered, the sum of these constituting  
1076 the acoustic signal. The signal amplitude  $R$  resulting in the sum of the channels is described  
1077 as a Rayleigh law.

1078 
$$R = \sqrt{X^2 + Y^2}$$

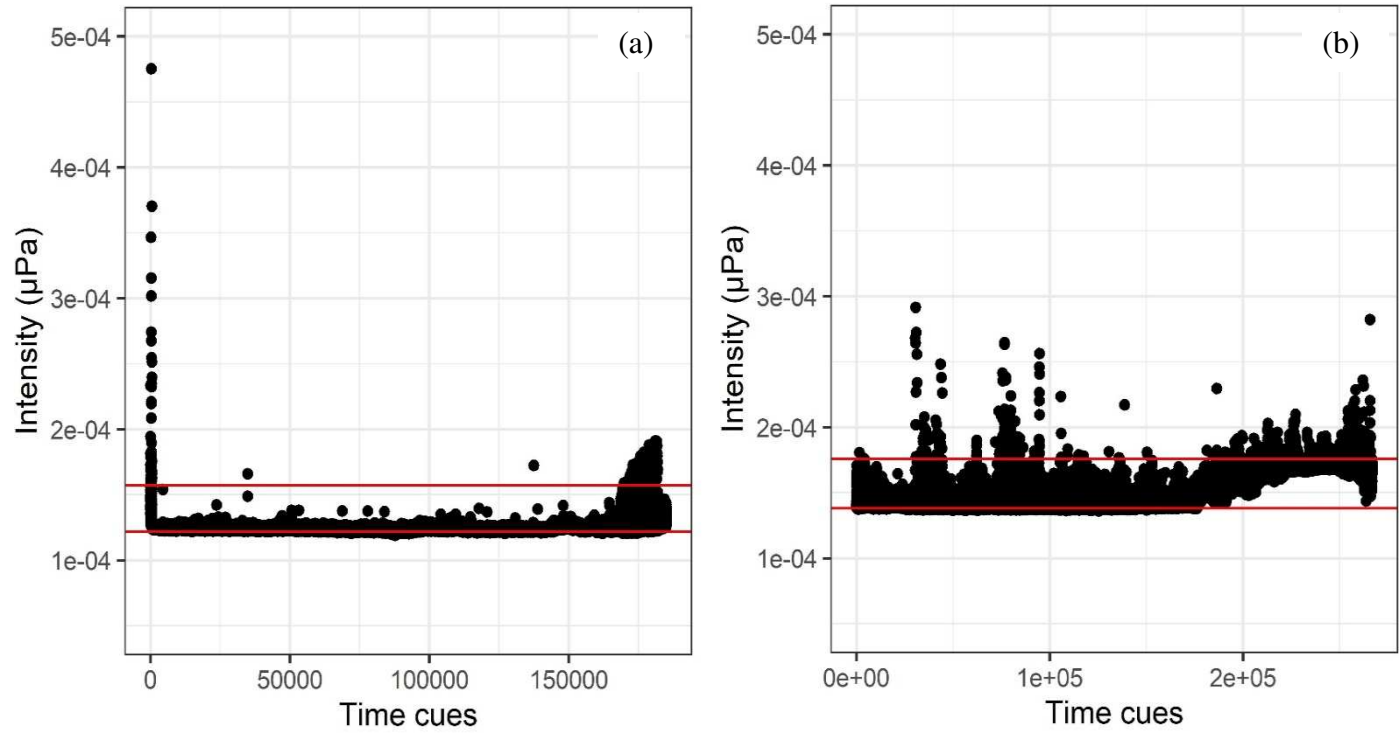
1079 with  $X \sim \mathcal{N}(0, \sigma^2)$  and  $Y \sim \mathcal{N}(0, \sigma^2)$

1080 Then  $R \sim \text{Rayleigh}(\sigma)$

1081

1082 A random sampling of the BNL is operated over the entire record, with 1000 pixels values  
1083 (acoustic power) sampled over a continuous sonar record sequence of at least 10 minutes.

1084 The sizes of the samples for KER and PV records are  $10 \cdot 10^7$  and  $13 \cdot 10^7$  respectively. The  
1085 cumulative distribution function of the Rayleigh law is fitted upon the BNL samples (Figure  
1086 2). The threshold is set as the acoustic power value ( $\mu\text{Pa}$ ) corresponding to the 99.9<sup>th</sup>  
1087 percentile of the Rayleigh distribution (for KER and PV), allowing the discrimination  
1088 between the actual target detection and the white noise in the studied range 1-1.5m of the  
1089 sonar beam.



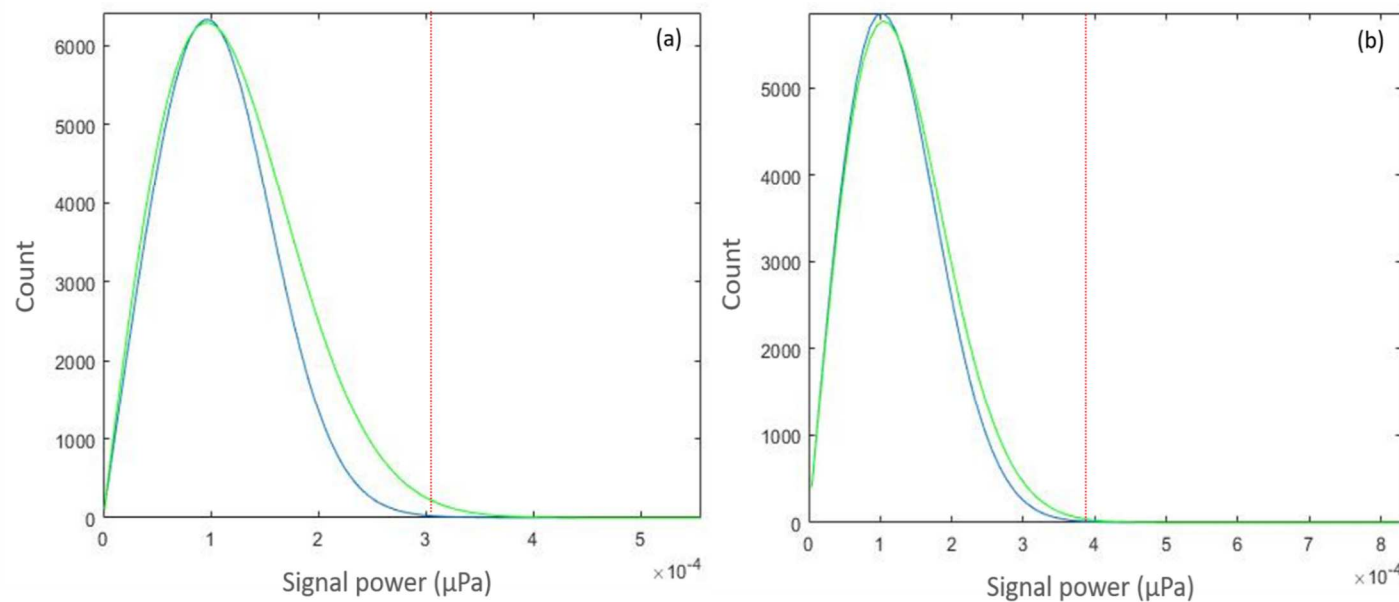
1091

1092 Figure 1: Time series of the Background Noise Level (BNL) for (a) KER and (b) PV. The  
 1093 interval between the red lines contains 99,9% of the sampled echoes, which are used to fit the  
 1094 Rayleigh distribution.

1095

1096 The far range of the sonar beam is unlikely to insonify target. But it could sometimes happen  
 1097 that the far range contains a few targets, particularly in regions with high target densities. The  
 1098 evolution of the background sampled values is represented in Figure 1. To prevent the  
 1099 influence of peaks or trends in the signal, the 1 % of extreme values are removed to prevent  
 1100 the influence of peaks or trends in the BNL threshold calculation.

1101



1102 Figure 2: Rayleigh fit of the data for KER (a) and PV (b) Background Noise Level (BNL)  
1103 sampled in the last meter of the signal range. The green line represents the density probability for  
1104 a theoretical Rayleigh distribution, and the blue lines the fitted distribution of the samples. The  
1105 vertical dotted red lines represent the defined threshold, set as the quantile 99,9% of the Rayleigh  
1106 distribution.

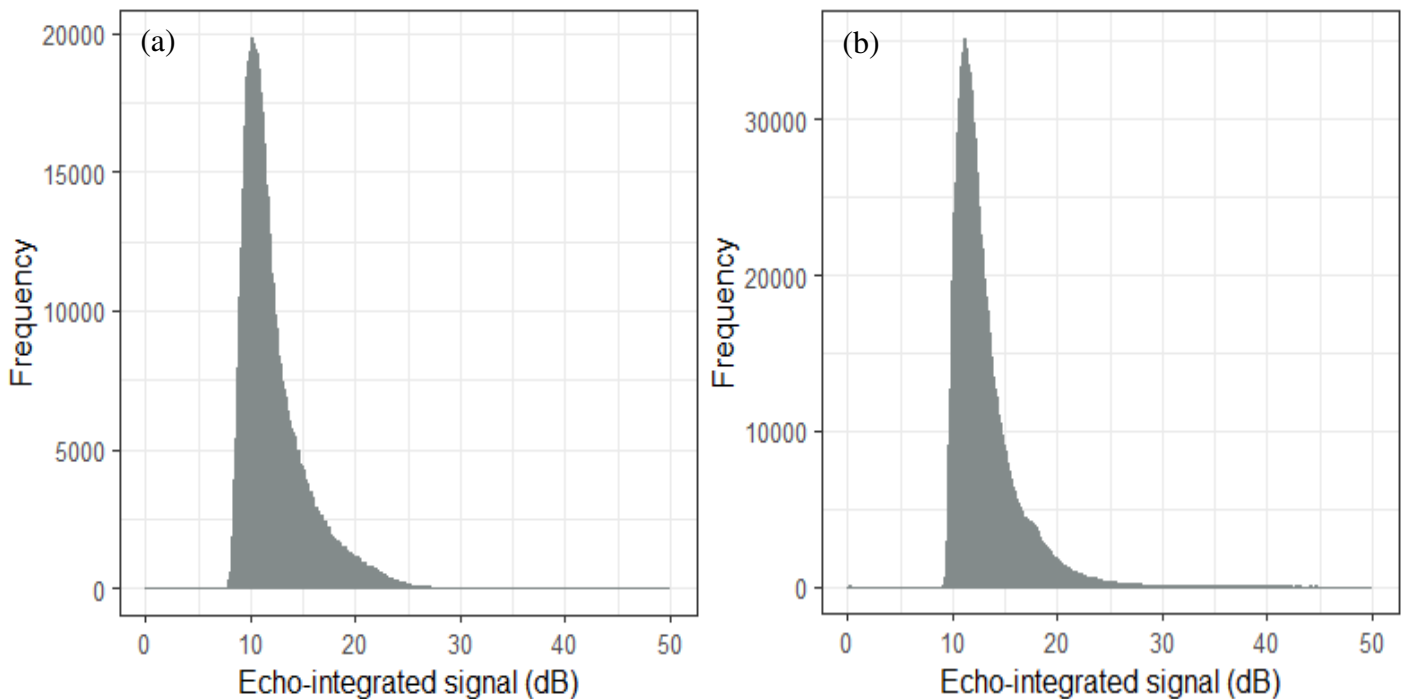
1107

#### 1108 Echo Intensity distribution

1109 The echo intensity presented in figure 3 is expressed as the echo-integration of each ping of the  
1110 records. The echo-integration is performed by summing the echo power of each 4mm bin

1111 insonified in the range 1m – 1.5m.

1112



1113 Figure 3: Distribution of the echo integrated intensities for (a) KER and (b) PV sonar records.

1114

#### 1115 Minimum size detected

1116 The ability of the sonar to detect small targets at the limit of the sensor resolution depends

1117 primarily on its position in the beam and the acoustic backscattering properties of its body.

1118 However, size is the most common measure to discriminate organisms, but fluid-like organisms

1119 - even of large size - cannot be observed, thus we propose a limit of detectability for small

1120 targets with high Signal-to Noise-Ratio.

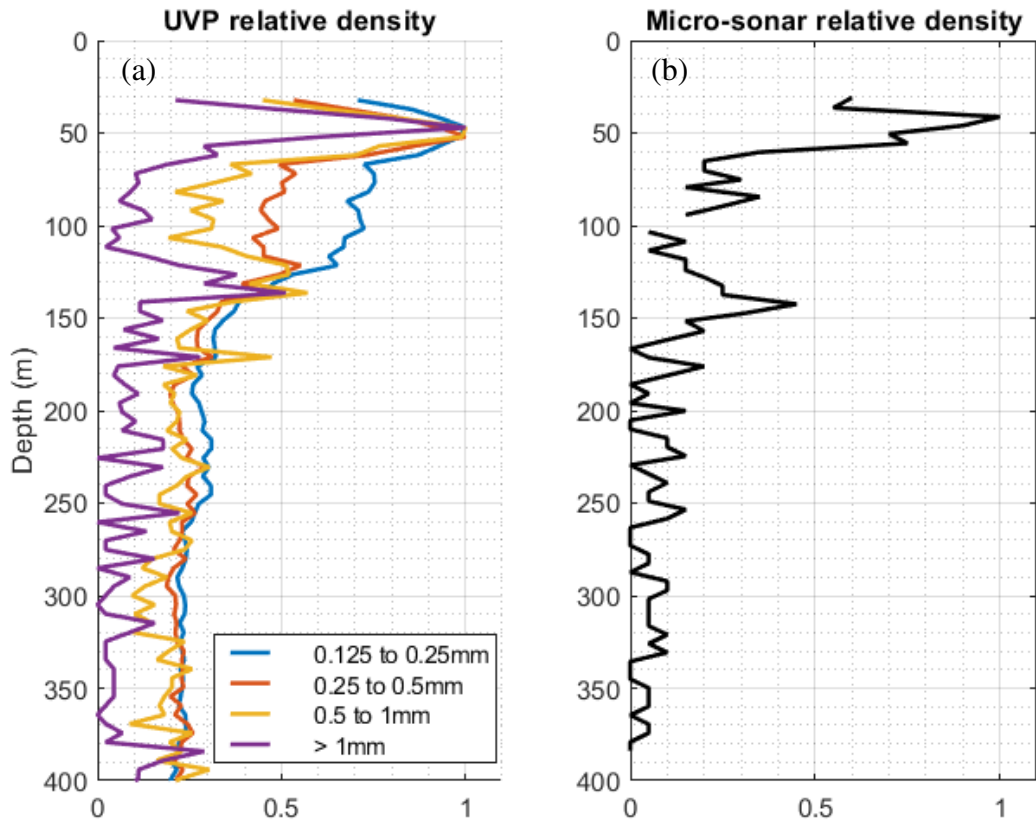
1121

1122 The sonar was deployed simultaneously with an optical sensor (Underwater Vision Profiler

1123 UVP5) in the Mediterranean Sea for an efficient measurement of the size of the targets. The

1124 density profiles show a maximum correlation for a target size class greater than 1mm, with the  
1125 same density peaks at 47.5m and 147.5m deep for both instruments (Figure 4). Targets  
1126 identified as detritus from the UVP images contribute to a large part of the signal and suggest  
1127 that they are detectable by sonar for sizes larger than 1mm.

1128



1129

1130 Figure 4: Relative density of detected targets simultaneously by (a) an Underwater Vertical  
1131 Profiler (UVP) and (b) the sonar tag attached to the UVP along a vertical profile. Colored curves  
1132 represent the relative density of detected targets belonging to a specific size class.

1133

1134

### 1135 Dives clustering:

1136 A dive is considered when the animal is continuously deeper than 15m. After the B-spline

1137 reconstruction and the FPCA performed on the B-spline coefficients, the observations

1138 (profiles) were projected in the space of the first two PCs (Figure 5). The five first

1139 components explained 98% and 91.5% of the total inertia for KER and PV respectively.

1140 By adding or subtracting the eigenfunctions to the mean profile, one can assess the effect of

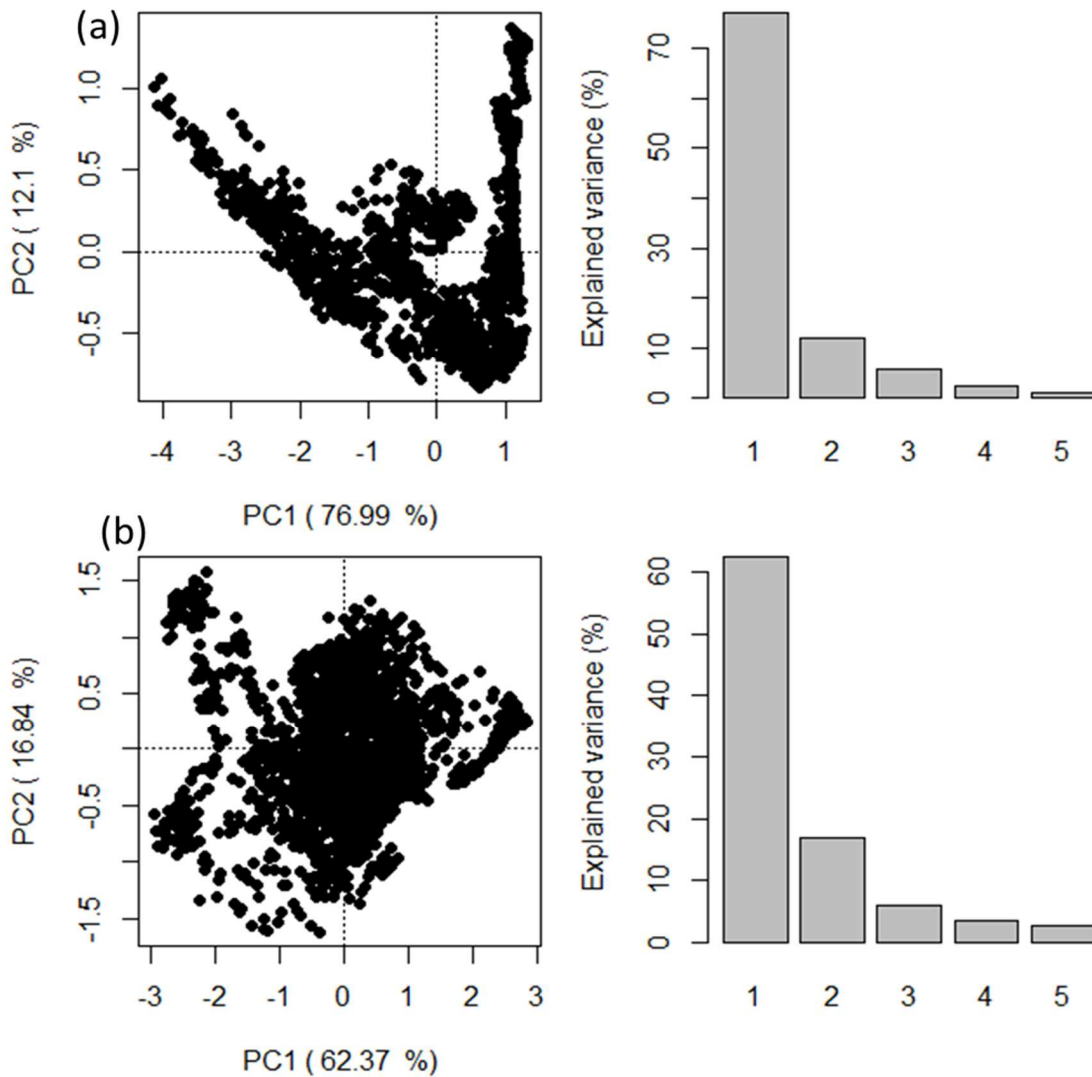
1141 the principal components on the curve shape (Figure 6). For each component, if an

1142 observation is in the positive part of the PC axis, the shape of this observation should be close

1143 to the one described by the '+' curve. Inversely, negatives observations on the PC axis would  
1144 have a curve close to the one described by the '-'.  
1145

1146 Before the  $k$ -means classification, the optimal number of  $k$  clusters was determined using the  
1147 Ward distance, minimizing the total within-cluster variance, on the observations. A visual  
1148 assessment of the cluster tree allowed retaining 3 clusters for both KER (Figure 7) and PV  
1149 (Figure 8).

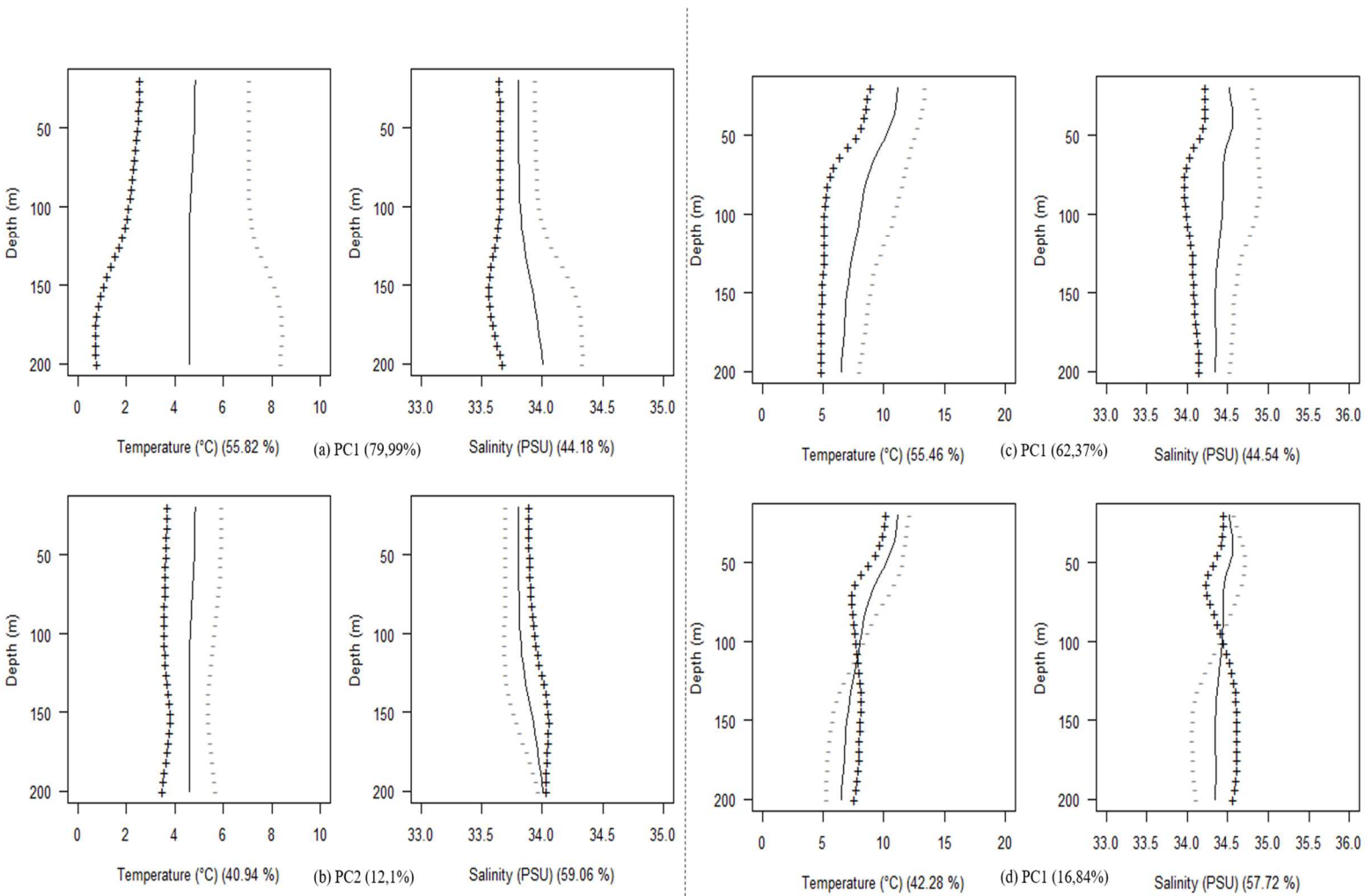
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1150  
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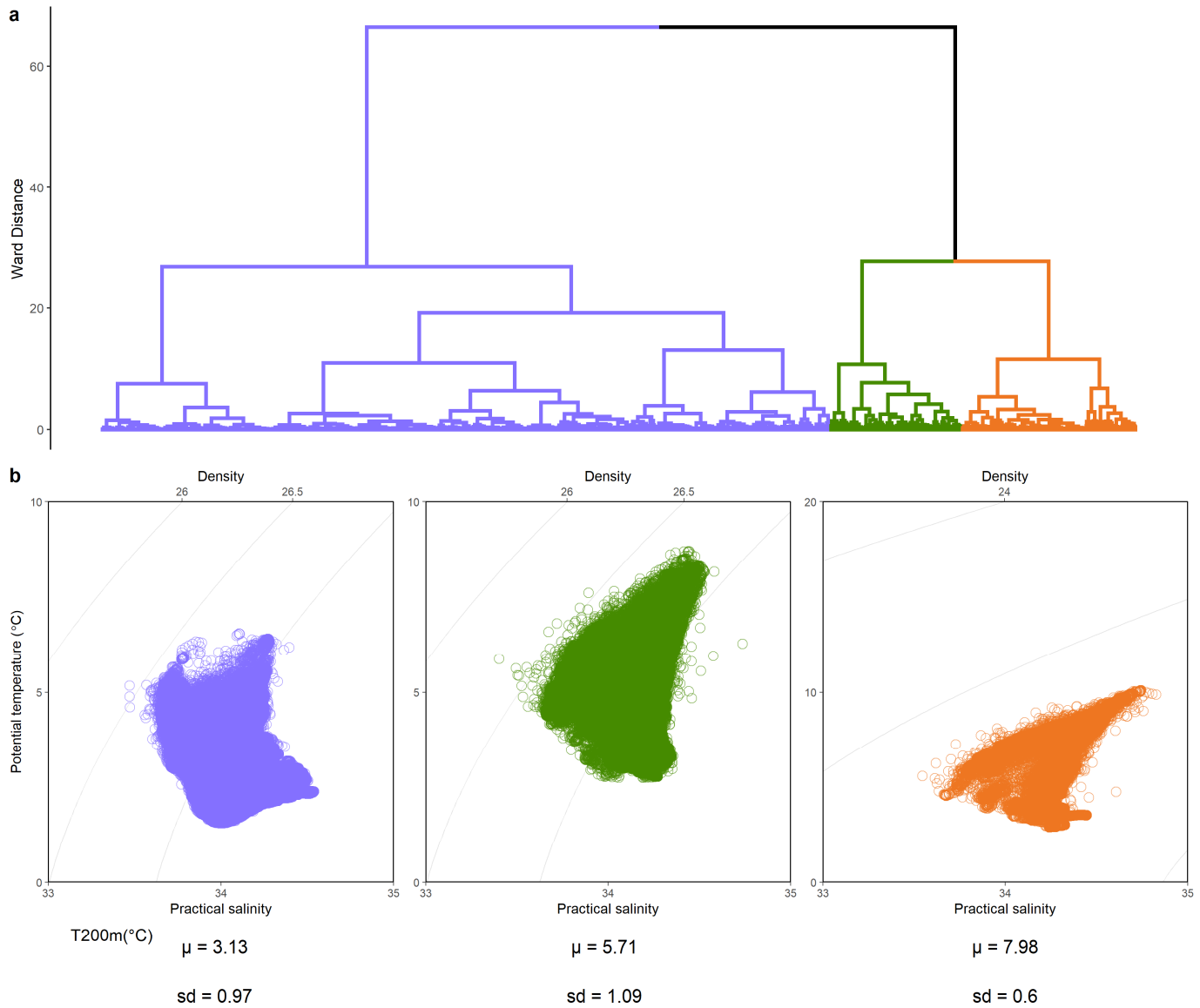
1152 Figure 5: Left: Temperature-Salinity profiles represented over the space of the first two modes of  
1153 the FPCA for KER (a) and PV (b). Right: Percentage of the variance explained by the first 5  
1154 eigenfunctions of the FPCA.

1155

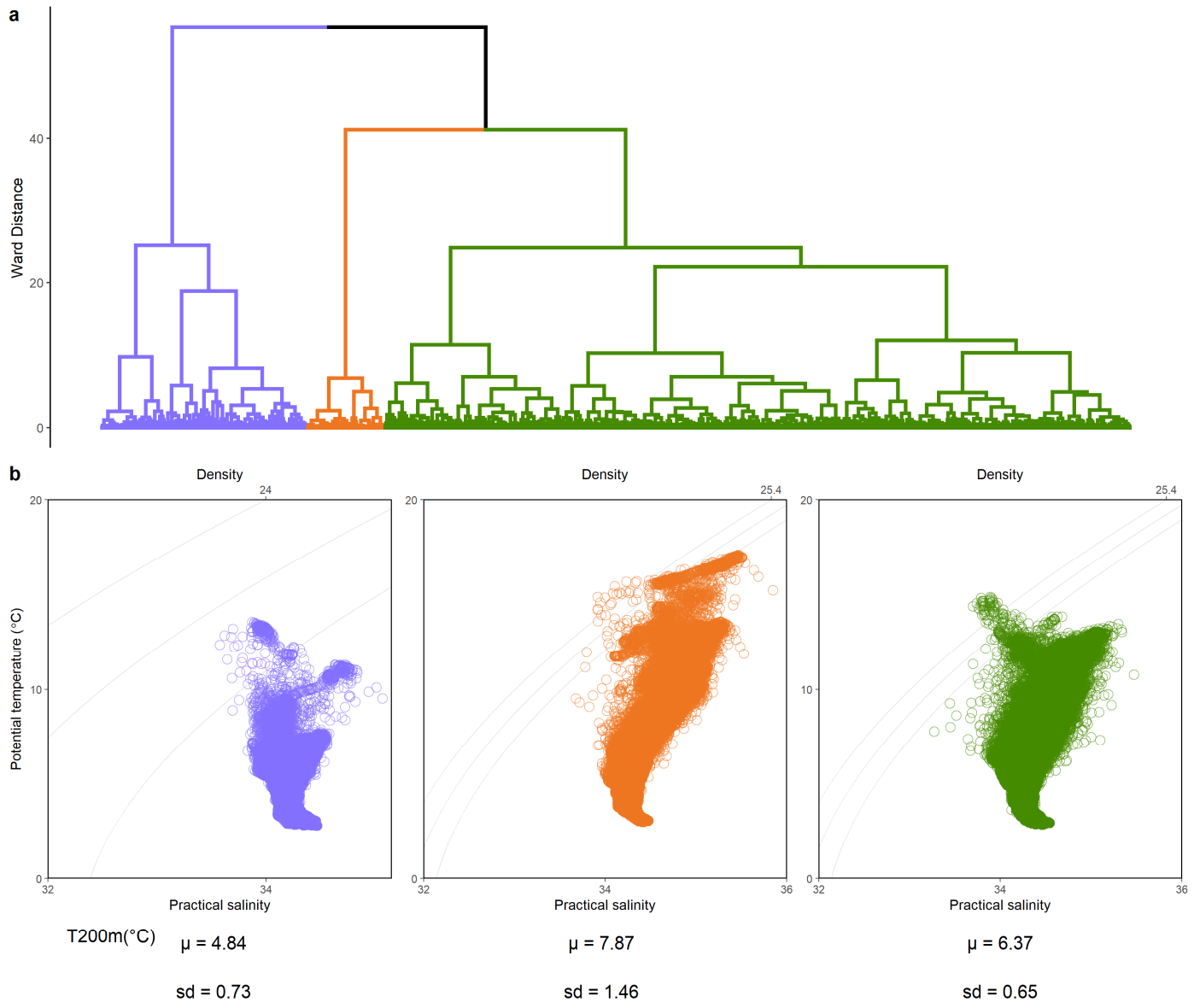


1156 Figure 6: Representation of the effects of the first two eigenfunctions on temperature and salinity  
 1157 mean profiles, for KER (a,b) and PV (c,d). The curves show the mean profile (solid) and the  
 1158 effect of adding (+) and subtracting (-) the first (a,c) and the second (b,d) eigenfunctions. The  
 1159 percentages indicated in the x-axis label are the variance contained by each variable (T and S)  
 1160 for the corresponding component.





1162 Figure 7: Cluster resulting of the *k*-means classification for KER. The hierarchical clustering  
 1163 tree, defined by the Ward distance, suggesting an optimal clustering in 3 groups: cluster 1  
 1164 (purple), cluster 2 (orange), and cluster 3 (green). (b) T-S diagrams of all profiles contained in  
 1165 each cluster, associated with the mean 200m-deep and the standard deviation of the temperature.



1167

1168 Figure 8: Cluster resulting of the *k*-means classification for PV. The hierarchical clustering tree,

1169 defined by the Ward distance, suggesting an optimal clustering in 3 groups: cluster 1 (purple),

1170 cluster 2 (orange), and cluster 3 (green). (b) T-S diagrams of all profiles contained in each

1171 cluster, associated with the mean 200m-deep and the standard deviation of the temperature.

1172

1173

1174 Table 1: Mean temperature and salinity with standard deviations recorded at 200m deep for

1175 each water masses in both locations.

Location	KERGUELEN			PENINSULA VALDES		
Cluster (water mass)	1	2	3	1	2	3
Temperature	3.1°C	5.7°C	8°C	4.8°C	6.4°C	7.9°C

(T200m)	(±0.1)	(±1.1)	(±0.6)	(±0.7)	(±0.6)	(±1.4)
Salinity	33.9‰	34.1‰	34.4‰	34.2‰	34.4‰	34.6‰
(S200m)	(±0.08)	(±0.14)	(±0.1)	(±0.07)	(±0.2)	(±0.3)

1176  
1177  
1178