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## Spies of the deep: An animal-borne active sonar and bioluminescence tag to characterise mesopelagic prey size and behaviour in distinct oceanographic domains

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# Spies of the deep: An animal-borne active sonar and bioluminescence tag to characterise mesopelagic prey size and behaviour in distinct oceanographic domains

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1 **Spies of the deep: an animal-borne active sonar and bioluminescence tag**  
2 **to characterise mesopelagic prey size and behaviour in distinct**  
3 **oceanographic domains**

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13 MC, TJDD, CG: conceptualization

14 MC, TJDD, PG, NF, CG, BP: methodology

15 MC, CC: formal analysis

16 MC, PG, BP: data curation

17 MC: writing – original draft

18 MC, TJDD, PG, NF, CC, BP, CG: writing – review and editing

19 TJDD, CG: supervision

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### 31 **Conflict of interest**

32 The authors declare that there is no conflict of interest.

### 33 **Abstract**

34 Mesopelagic fishes, a central component of marine trophic networks, play a  
35 fundamental role in marine ecosystems. However, as they live in highly inaccessible  
36 environments, little information is currently available on their distribution and  
37 abundance. The emergence of biologging technologies has made it possible to use  
38 deep-diving predators as bio-samplers of their environment in under-sampled regions.  
39 In this work, we deployed an innovative miniaturised sonar tag that combines active  
40 acoustics with high-resolution GPS, pressure, movement and light sensors on  
41 Southern elephant seals, a deep-diving predator feeding on mesopelagic prey. Seals  
42 were also equipped with Conductivity-Temperature-Depth tags tags. Salinity and  
43 temperature depth profiles were used to define oceanographic domains, allowing us to

44 explore distribution and ecology of mesopelagic prey targeted by seals and the seals'  
45 foraging behaviour. We highlighted strong vertical differences in prey characteristics  
46 and behaviour, with larger, more evasive and less bioluminescent prey in deeper  
47 waters. Moreover, prey encountered in warmer waters were found deeper, were more  
48 evasive and displayed a more marked diel vertical migration behaviour compared to  
49 prey encountered in colder waters, suggesting that prey accessibility and  
50 characteristics differ according to oceanographic domains. This study highlights the  
51 usefulness of the sonar-bioluminescence tag to infer mesopelagic prey distribution and  
52 habitat when deployed on deep-diving predators such as elephant seals.

### 53 **Keywords**

54 Southern elephant seals; *Mirounga leonina*; mesopelagic; myctophids; biologging.

## 55 **1. Introduction**

56 Mesopelagic fishes represent the largest vertebrate biomass on Earth (Hidalgo and  
57 Browman, 2019; Irigoien et al., 2014; Proud et al., 2019) and play a fundamental role  
58 in marine ecosystems. They are a central component in the marine trophic network,  
59 allowing energy transfers between low trophic levels, i.e. phyto and zooplankton, and  
60 upper trophic levels, i.e. predators (Cherel et al., 2010). Most mesopelagic fishes  
61 perform diel vertical migrations, moving up to the surface at night and going back to  
62 deep waters during the day (Catul et al., 2011), and thus play a key role in the carbon  
63 pump by facilitating carbon transfer from the surface to deeper ecosystems (St. John  
64 et al., 2016). However, despite their ecological importance, the ecology of mesopelagic  
65 fishes remains poorly known, particularly because they live in highly inaccessible  
66 environments. From the perspective of predicting the effects of climate change on

67 marine ecosystems, there is a need to increase our knowledge on the influence of  
68 environmental parameters on their distribution. Changes in temperature of the whole  
69 water column could potentially affect vertical migration of mesopelagic fish. Therefore,  
70 there is a need to understand how mesopelagic fishes behave in different thermal  
71 environments to better understand changes in ecosystems, including impacts on their  
72 predators.

73 Usual methods to study mesopelagic communities include net sampling and acoustic  
74 surveys. Net sampling consists of deploying a net from an oceanographic research or  
75 fishing vessel in order to collect part of the individuals present in the area with the aim  
76 of making an inventory of the species, estimating size of individuals and their biomass.  
77 However, net avoidance is commonly observed in mesopelagic fishes, leading to a  
78 bias in the species collected (Irigoien et al., 2014; Kaartvedt et al., 2012). Moreover,  
79 numerous trawls at different depths are necessary to obtain detailed information on the  
80 distribution of species, which can be challenging. In contrast, acoustic surveys  
81 describe the fine-scale distribution of organisms in the water column. Most  
82 oceanographic research vessels are equipped with on-board echosounders that emit  
83 successive sound pulses reflected off any object they encounter in the water column  
84 (Misund, 1997). Active acoustics thus provides detailed information on the distribution  
85 of organisms with limited effect on their behaviour. However, low-frequency acoustic  
86 waves used in oceanographic vessels to sample a large part of the water column do  
87 not provide detailed echoes of the insonified objects (Misund, 1997). This limits the  
88 usefulness of echosounders to obtain fine-scale data on organisms in deeper parts of  
89 the water column. Moreover, both acoustic surveys and net samplings require  
90 expensive, time-consuming and logistically demanding oceanographic campaigns,

91 that can be highly challenging to set up in remote areas such as polar regions, limiting  
92 spatial and temporal coverage.

93 Recent developments of biologging technologies, i.e. devices attached on animals to  
94 record information about their behaviour and ecology (Rutz and Hays, 2009), have  
95 largely increased our understanding of the ecology of marine predators and their  
96 environment (e.g. Guinet et al., 2014, 2001; Slip et al., 1994; Yoshino et al., 2020). By  
97 integrating high-resolution oceanographic sensors such as temperature, salinity, light  
98 or chlorophyll a sensors in tags that can be attached on large deep-diving predators,  
99 these predators can be used as bio-samplers of their environment (Fedak, 2013;  
100 Harcourt et al., 2019; Treasure et al., 2017), making it possible to collect environmental  
101 data in under-sampled regions. These data are most valuable when deployed with  
102 animal telemetry tags so that the environmental data can be confidently and  
103 simultaneously mapped. Investigating the foraging ecology, i.e. at-sea distribution,  
104 diving behaviour and diet of marine predators also provide information on their cryptic  
105 and generally poorly known prey (Cherel et al., 2008). In that context and among deep-  
106 diving predators, Southern elephant seals (*Mirounga leonina*, Linnaeus 1758, SES  
107 hereafter) are of special interest. SES breed on sub-Antarctic islands and alternate at-  
108 sea periods to feed and on-land periods to breed and moult. During their months-long  
109 foraging trips, SES travel great distances, up to thousands of kilometres, and perform  
110 continuous dives at depths ranging generally from 200 to 1000 m, and up to 2000 m  
111 during ~ 20 min. Therefore, by covering large horizontal and vertical ranges, SES are  
112 an ideal species to sample environmental conditions in these remote areas (e.g.  
113 Bailleul et al., 2007; Charrassin et al., 2010; Dragon et al., 2010; Guinet et al., 2014;  
114 Tournier et al., 2021). SES have become a major component in the observation of the  
115 Southern Ocean oceanographic conditions (Fedak, 2013). While adult males forage

116 mostly on benthic and benthopelagic prey such as squids, young males and adult  
117 females mainly target mesopelagic prey such as myctophids (Cherel et al., 2008).

118 Deploying high-resolution movement sensors such as accelerometers on deep-diving  
119 predators allows for identifying prey capture attempts (Suzuki et al., 2009; Viviant et  
120 al., 2010; Ydesen et al., 2014), providing valuable information on horizontal and vertical  
121 distribution of mesopelagic prey targeted by these predators (Guinet et al., 2014).

122 However, fine-scale information on prey, such as their size or behaviour remain  
123 challenging to obtain. Miniaturised video cameras can be attached to marine predators  
124 foraging in clear and shallow waters (e.g. Goldbogen et al. (2017) on blue whales  
125 *Balaenoptera musculus*; Papastamatiou et al. (2018) on white-tip sharks *Carcharhinus*  
126 *longimanus*; Semmens et al. (2019) on white sharks *Carcharodon carcharias*).

127 However, SES often forage in the aphotic zone. Using a light source in these deep  
128 waters can significantly alter both predator and prey behaviours (Geoffroy et al., 2021;  
129 Rooper et al., 2015; Ryer et al., 2009), limiting the usefulness of video cameras to  
130 collect meaningful data about prey characteristics and behaviour. The increased power  
131 consumption of the tag limits recording duration to a few hours of foraging, while  
132 foraging trips can last several months, providing short, but important, glimpse on the  
133 prey and foraging behaviour of those species. Very recently, an innovative miniaturised  
134 sonar tag has enabled a step forward in the study of fine-scale biotic environment in  
135 cryptic marine predators. This state-of-the-art tag, inspired by a toothed whale  
136 echolocation system, uses a high-click rate narrow, forward directed beam that can  
137 insonify prey at a distance up to 6 m in front of the animal. Data recorded by this tag  
138 provide information on prey aggregation type, escape behaviour and acoustic size  
139 without altering either predator or prey behaviour (Goulet et al., 2019). A more recent  
140 version of the sonar tag also includes a light sensor specifically developed to study



141 bioluminescent behaviour of prey (Goulet et al., 2020), offering a unique opportunity to  
142 accurately describe behaviour and characteristics of prey targeted by aphotic and  
143 cryptic marine predators (Chevallay et al., 2023).

144 The aim of this study was to provide a better understanding of the distribution and  
145 habitat of mesopelagic prey targeted by SES. Previous studies showed that seals visit  
146 different areas with contrasted oceanographic conditions during their foraging trips  
147 (Bailleul et al., 2007; Biuw et al., 2007) and that seals targeting distinct oceanographic  
148 domains differed in their foraging efficiency (Guinet et al., 2014; Richard et al., 2016).  
149 Using an innovative method to identify functional oceanographic domains (FOD  
150 hereafter) according to their temperature and salinity profiles recorded by conductivity-  
151 temperature-depth (CTD) tags (Fonvieille et al., 2023; Pauthenet et al., 2017; Tournier  
152 et al., 2021) deployed simultaneously with sonar tags on female SES, we aimed at  
153 exploring the functional relationships between oceanographic parameters, distribution  
154 and ecology of mesopelagic prey targeted by seals and the seals' foraging behaviour.  
155 We predicted that each FOD would be home to prey with diverse characteristics and  
156 behaviour, and that some habitats would have more favourable prey accessibility  
157 and/or prey quality (i.e. larger or less evasive prey). Specifically, we hypothesised that  
158 prey tend to be more evasive in warmer FOD but also less accessible, as suggested  
159 by Guinet et al. (2014) and Richard et al. (2016).

## 160 2. Material and methods

### 161 2.1. Device deployments and data collection

162 Data were collected on 9 post-breeding female Southern elephant seals in October  
163 2018 (n = 3), October 2019 (n = 3) and October 2020 (n = 3), in Kerguelen Islands  
164 (49°20'S – 70°26'E). Females were captured with a canvas head-bag, anaesthetized

165 with a 1:1 combination of Tiletamine and Zolazepam (Zoletil 100 – 0.7 to 0.8 ml/100  
166 kg) either injected intravenously (McMahon et al., 2000) or using a deported  
167 intramuscular injection system. Females were measured to the nearest centimetre and  
168 weighted to the nearest kilogram. They were equipped with a neck-mounted Argos tag  
169 (SPOT-293 Wildlife Computers, 72x54x24 mm, 119 g in air), a back-mounted CTD tag  
170 (SMRU-SRDL, 115x100x40 mm, 680 g in air) and either a head-mounted DTAG-4  
171 sonar tag (n = 7, 95x55x37 mm, 200 g in air, see Goulet et al. (2019) for further details  
172 on the device) or a DTAG-4 sonar-light tag (n = 2, 92x69x37 mm, 250 g in air). Tags  
173 were glued to the fur using quick-setting epoxy glue (Araldite AW 2101, Ciba). CTD  
174 tags recorded conductivity, temperature and depth at 0.5 Hz. Sonar and sonar-light  
175 tags were programmed to sample GPS position (up to every minute at surface), tri-  
176 axial acceleration (200 Hz), tri-axial magnetometer (50 Hz) and pressure (50 Hz).  
177 Sonar-light tags also integrated a light sensor specifically designed to sample  
178 bioluminescence events with a sampling frequency of 50 Hz (Goulet et al., 2020). The  
179 active sonar within the tags recorded acoustic backscatter returning from 10  $\mu$ s pings  
180 with a centre frequency of 1.5 MHz, at a 25 Hz ping rate for 2018 and 2019  
181 deployments and 12.5 Hz for 2020 deployments. The active sonar operated with a 3.4°  
182 aperture beam width and a 6 m range (Goulet et al., 2019). Sonar and sonar-light tags  
183 were set to record data one day out of two to increase recording duration. Tags were  
184 recovered in late December to January when females returned to shore to moult using  
185 the same capture and sedation methods. All experiments were conducted under the  
186 ethical regulation approval of the French Ethical Committee for Animal  
187 Experimentations (2019070612143224 (#21375)) and the Committee for Polar  
188 Environment.

## 189 2.2. Foraging behaviour

190 Sonar, movement and location data recorded by the sonar tags were analysed using  
191 custom-written codes and functions from [www.animaltags.org](http://www.animaltags.org) in MATLAB version  
192 2022b (The MathWorks, 2022). Statistical analyses were conducted in R software  
193 version 3.5.1 (R Core Team, 2018). GPS tracks were plotted in a map using QGIS  
194 version 3.10 (QGIS Development Team, 2019). Diving behaviour was assessed by  
195 using pressure data recorded by the sonar tags. Seals were considered as diving when  
196 depth exceeded 20 m.

## 197 2.3. Prey capture attempt identification

198 Prey capture attempts (PrCAs hereafter) were detected from the full 200 Hz tri-axial  
199 acceleration data recorded by the sonar tags, by computing the norm of the differential  
200 of the tri-axial acceleration (norm-jerk hereafter) (Chevallay et al., 2023). Histograms  
201 of the norm-jerk showed a clear bimodal distribution for all seals. High jerk modes  
202 associated with prey strikes were separated from the lower modes using a threshold  
203 at  $400 \text{ m.s}^{-2}$ . Therefore, spikes in the norm-jerk higher than  $400 \text{ m.s}^{-2}$  were classified  
204 as PrCAs. As prey may be encountered in patches or may elude capture, leading to a  
205 bout structure in prey strikes, strikes occurring less than 15 s from the previous strike  
206 were grouped in the same bout according to the distribution of the inter-strike interval  
207 (Chevallay et al., in revision). Bout duration was defined as the time elapsed between  
208 the first and last strike of the bout.

## 209 2.4. Functional oceanographic domain identification

210 Different functional oceanographic domains were identified using SES in situ  
211 temperature and salinity (TS) profiles. The domains were defined following the  
212 procedure described in Fonvieille et al. (2023). The method belongs to functional data

213 analysis, working on the shape of the profiles (Ramsay and Silverman, 2005). As the  
214 method requires profiles of fixed depth range, we decided to work on profiles between  
215 20 and 200 m as done in Tournier et al. (2021). This choice implied the removal of all  
216 profiles not reaching a depth of 200 m but came as a compromise between capturing  
217 a large part of the TS vertical variability (Appendix A) and retaining a large proportion  
218 of SES data. Here, the depth of 200 m was selected to maximise spatiotemporal  
219 coverage, especially at night when SES perform shallower dives (Tournier et al., 2021).

220 The profiles were first generated on a constant vertical grid from 20 to 200 m for each  
221 dive using temperature and salinity data collected by the CTD tags. We then  
222 transformed the discrete TS profiles into functions  $x(z)$  using a decomposition on a  
223 cubic B-splines basis. Each profile  $n$  was expressed as a linear combinations of  $K$   
224 basis functions  $\phi_k(z)$ :

$$225 \quad x_n^i(z) = \alpha_1 \phi_1(z) + \alpha_2 \phi_2(z) + \dots + \alpha_K \phi_K(z), i \in \{T, S\}, n = 1, \dots, N,$$

226 with  $N$  the total number of profiles. The coefficients of the decomposition  $\alpha_k$  were  
227 estimated by polynomial regression (R package “fda”, (Febrero-Bande and De La  
228 Fuente, 2012)), they hold the curve’s information (i.e. min, max, shape). A basis of  $K$   
229 = 20 coefficients was chosen to keep sufficient vertical complexity without overfitting  
230 the data. The resulting temperature and salinity B-splines coefficients were joined end  
231 to end in a table  $X$  of size  $N \times 2K$ .

232 A bivariate functional principal component analysis (FPCA, R package “fda”) was  
233 applied on the coefficients to extract principal modes of variability in the curves shapes.  
234 As in a principal component analysis, the FPCA decomposes the table  $X$  into principal  
235 components (PC) that correspond to uncorrelated linear combinations of the original

236 variables, maximizing the variance (see Ramsay and Silverman (2005); Pauthenet et  
237 al. (2017) and Nerini et al. (2022) for more details).

238 Finally, a model-based clustering (Bouveyron et al., 2019) was applied on the first PCs  
239 of the FPCA to gather TS profiles sharing similar thermohaline vertical structure (R  
240 package “mclust”, (Scrucca et al., 2016)). The appropriate number of clusters was  
241 defined using the Bayesian Information Criterion (Schwarz, 1978) and the Integrated  
242 Completed Likelihood (Biernacki et al., 2000). The resulting clusters were considered  
243 as representing different FOD and were plotted along the track of SES.

244 2.5. Prey characteristics and behaviour

245 2.5.1. Sonar data analysis

246 2.5.2. Sonar data recorded during bouts were displayed as echograms, showing  
247 the time on the horizontal axis and the distance from the sonar tag on the  
248 vertical axis, extending from 10 s before the bout start time to 2 s after the  
249 bout end time. Because of the large number of bouts detected (ranging from  
250 4595 to 12039 per animal), only a random subsample of 5 to 10% of bouts  
251 performed during acoustic data recordings were analysed. Three different  
252 variables describing predator-prey interactions were extracted manually  
253 from echograms (Appendix B) First, the number of prey was defined as the  
254 maximum number of independent echo traces within a same ping (Jones et  
255 al., 2008). It was scored as one, two or more than two, i.e. a school of prey.  
256 Second, prey escape behaviour was identified from the closing speed  
257 between predator and prey, which will vary in case of prey escape event,  
258 resulting in a change in the slope of the prey echo trace. Prey flight initiation  
259 distance was defined as the distance between the tag and the prey when  
260 prey first showed an escape reaction (Goulet et al., 2019; Vance et al.,  
261 2021). Third, prey acoustic size was estimated from duration of echo  
262 transients following Burwen et al. (2003). Specifically, the time during which  
263 the echo intensity was within 20 dB of its maximum value was multiplied by  
264 half of the sound speed to give a proxy for apparent prey size. The  
265 measurement was done ping-by-ping and we used the maximum of all  
266 measurements for the final size estimate. Echo duration was only measured  
267 on evasive prey on the assumption that escaping prey will typically be  
268 oriented parallel with the predator providing a relatively consistent  
269 orientation for which to estimate size. Bioluminescence data analysis

270 Bioluminescent flashes were defined as short high intensity spikes in the 50 Hz light  
271 data recorded by the sonar-light tags decimated at a 5 Hz sampling rate. Spikes in the  
272 data higher than 0.07 (arbitrary unit) were classified as flashes (Goulet et al., 2020).  
273 Flashes detected within less than 5 s of each other were considered coming from the  
274 same bioluminescence event (Goulet et al., 2020). If a bioluminescence event started  
275 between 5 s before and 5 s after the bout, it was considered associated with the bout.

## 276 2.6. Statistical analyses

277 For the following analyses, only data recorded on SES equipped with sonar-light tags  
278 were used for the comparisons between flashing and non-flashing prey, while  
279 comparisons between evasive and non-evasive prey were made using data recorded  
280 by all the sonar-tagged SES. Prey flashing behaviour was inferred for all bouts of the  
281 two SES equipped with sonar-light tags, while prey evasive behaviour was inferred for  
282 5-10% of bouts of all the sonar-tagged SES. For all subsequent models, assumptions  
283 were checked (i.e. autocorrelation, homoskedasticity) and any deviation from them  
284 were corrected in the models.

### 285 2.6.1. Inter-functional oceanographic domain differences in prey characteristics 286 and distribution

287 Prey accessibility, using the depth of bout as its proxy (Boyd et al., 2015; Jouma'a et  
288 al., 2016) was compared between FOD using LMM (R package nlme, (Pinheiro et al.,  
289 2017)) with dive depth as a response variable, FOD as the fixed effect and SES  
290 individual identities as a random effect during both day and night. To test for differences  
291 in prey behaviour according to FOD, the proportion of evasive versus non-evasive prey  
292 and flashing versus non-flashing prey was compared between FOD using generalised  
293 linear mixed models with binomial distribution (GLMM hereafter, R package lme4,



294 (Bates et al., 2015)). We used the proportion of each prey type as the response  
295 variable, FOD as the fixed effect and SES identities as a random effect. As the two  
296 seals equipped with sonar-light tag almost never visited FOD4, we did not compute the  
297 proportion of flashing prey in this FOD. Prey flight initiation distances (m) were  
298 compared between FOD using LMM with flight initiation distance as the response  
299 variable, FOD as the fixed effect and SES identities as a random effect. Bout duration  
300 (s), a proxy for prey capture difficulty, or an indication of multi-prey capture (Goulet,  
301 2020), was compared between FOD using LMM with bout duration as the response  
302 variable, FOD as the fixed effect and SES identities as a random effect. Finally,  
303 distribution of prey acoustic size was reconstructed for each FOD and were compared  
304 using a pairwise Kolmogorov-Smirnov test with Bonferroni correction for multiple  
305 testing.

#### 306 2.6.2. Intra-functional oceanographic domain differences in prey characteristics 307 and distribution

308 Inside each FOD, difference in depths at which prey were encountered between  
309 evasive and non-evasive prey and between flashing and non-flashing prey were  
310 compared using prey encounter depth as a response variable, prey type (evasive vs.  
311 non-evasive prey, flashing vs. non-flashing prey) as the fixed effect and SES individual  
312 identities as a random effect. To test the hypothesis that prey size varies with depth,  
313 prey acoustic size distributions were reconstructed for depth classes every 200 m, from  
314 20 to 1000 m, and were compared using Kolmogorov-Smirnov test with Bonferroni  
315 correction for multiple testing inside each FOD. Finally, the relationship between bout  
316 duration and bout depth was assessed for each FOD using a LMM with bout duration  
317 as a response variable, bout depth as the fixed effect and SES individual identifies as  
318 a random effect.

## 319 3. Results

### 320 3.1. Foraging behaviour and targeted prey

321 Tags recorded data during 29-79 days (Table 1). One GPS sensor and one CTD tag  
322 failed to record any data on individual ml18\_293a and individual ml19\_296a  
323 respectively so data recorded from these individuals were not used for spatial  
324 analyses. Over that period, seals performed  $69 \pm 7$  (mean  $\pm$  sd) dives per day (range  
325 57-79 dives per day), and  $511 \pm 53$  bouts/day (range 443-610 bouts/day). Seals  
326 performed dives  $418 \pm 93$  m deep for  $19 \pm 3$  min. A diel diving pattern was observed  
327 for almost all individuals, with deeper and longer dives performed during the day ( $456$   
328  $\pm 96$  m,  $21 \pm 4$  min) than during the night ( $331 \pm 75$  m,  $16 \pm 2$  min, LMM,  $P < 0.001$ ).  
329 Seals almost exclusively targeted single prey (99% of the targeted prey) while schools  
330 of prey represented only 1% of the targeted prey. Among single prey, 81% were  
331 evasive. For the two individuals equipped with sonar-light tags, flashing prey  
332 represented 24 and 29% of their targeted prey respectively. Prey acoustic size mainly  
333 distributed from 5.1 to 9.0 cm (1<sup>st</sup> and 3<sup>rd</sup> quartiles, Q1-Q3 hereafter), with a range of  
334 1.2-32.8 cm.

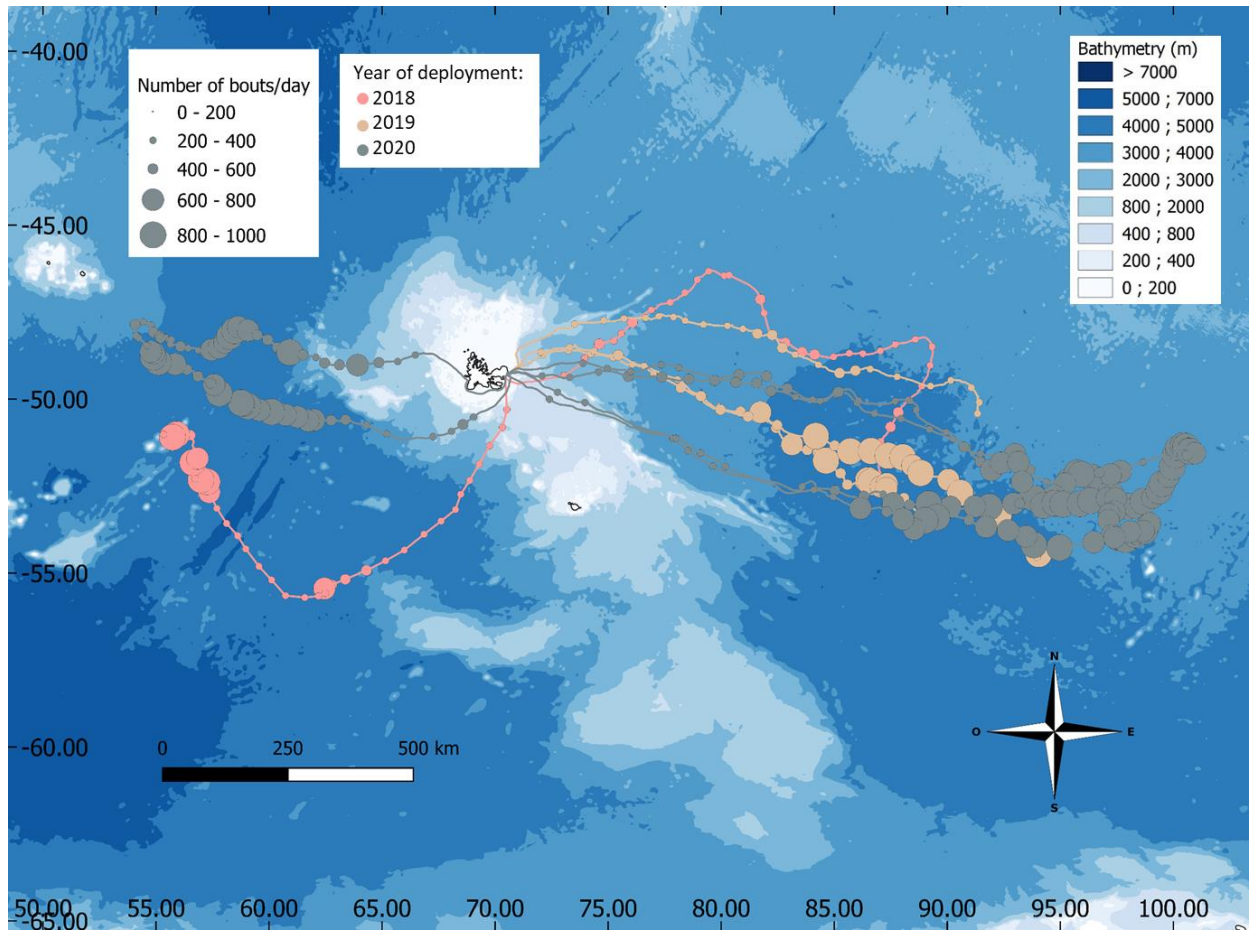
335 Table 1: Summary of field deployments: length (cm) and weight (kg), number of days  
336 of recordings, number of recorded dives and bouts of female SES from Kerguelen  
337 Islands equipped with either sonar or sonar-light tag during their post-breeding foraging  
338 trip. Seal ID comprises the two first letters of the Latin species binomial followed by the  
339 year and Julian day of attachment, and a letter denoting the sequential animal of day.

Seal ID	Weight (kg)	Length (cm)	Device	Number of days of recordings	Number of recorded dives	Number of recorded bouts
ml18_292a	237.5	226	sonar	43	3393	22223
ml18_293a	158.5	225	sonar	29	1760	6823
ml18_294a	249.5	226	sonar	35	2380	11694
ml19_295a	287.5	239	sonar	30	2096	14284
ml19_295c	321.5	237	sonar	35	2336	18885
ml19_296a	252.2	225	sonar	28	1752	8205
ml20_295a	380.0	268	sonar-light	77	7669	41439
ml20_296a	380.0	231	sonar-light	79	4535	40304
ml20_296c	380.0	196	sonar	73	5357	36684

340

### 341 3.2. Foraging area

342 All seals but two travelled east of the Kerguelen Islands (Figure 1). The two other seals  
343 travelled west. They concentrated their foraging activity at a mean distance from the  
344 shore of  $1170 \pm 539$  km (Q1-Q3: 789-1663 km, Figure 1).



345

346 Figure 1: GPS tracks of eight female SES from Kerguelen Islands equipped with high-  
 347 resolution sonar and movement tags in 2018 (n = 2, in pink), 2019 (n = 3, in beige) and  
 348 2020 (n = 3, in grey) during their post-breeding foraging trips (November-January).  
 349 Each point represents one day, with the size of the point being proportional to the  
 350 number of bouts performed that day. For females tagged in 2018 and 2019, the tags  
 351 stopped recording before the end of the foraging trip.

352 3.3. Inter-functional oceanographic domain differences in prey  
 353 characteristics and distribution

354 During their foraging trips, seals encountered four FOD that we identified from *in-situ*  
 355 temperature and salinity profiles recorded by CTD tags (Figure 2). These FOD were  
 356 distributed along an increasing temperature gradient from FOD 1 to FOD 4, with little

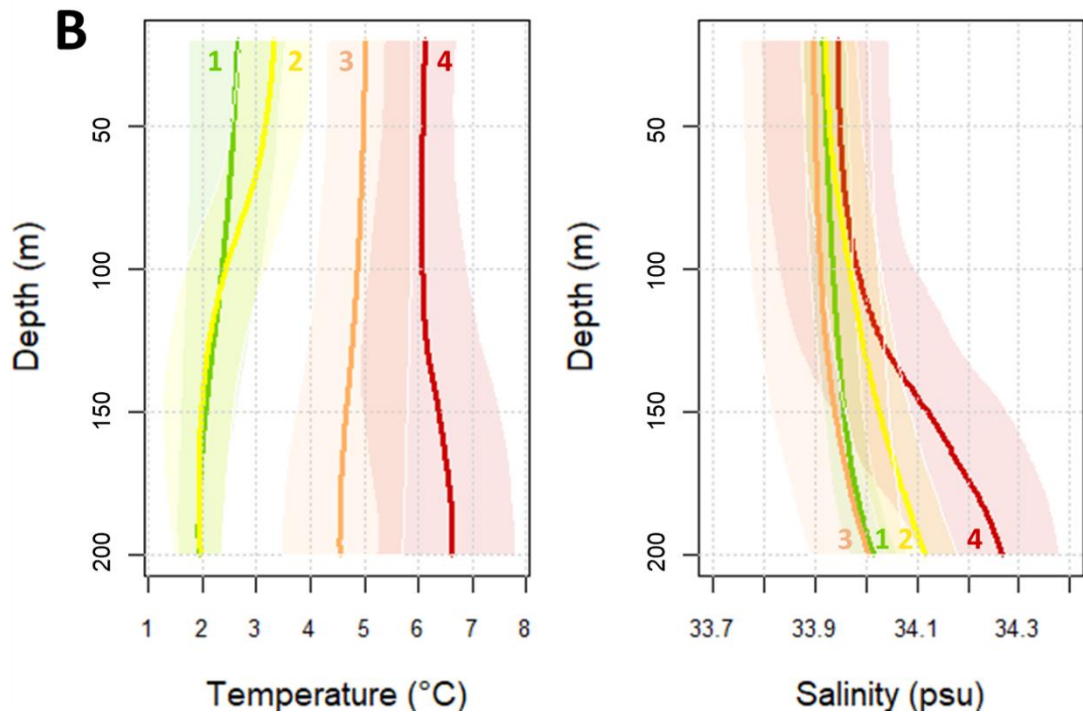
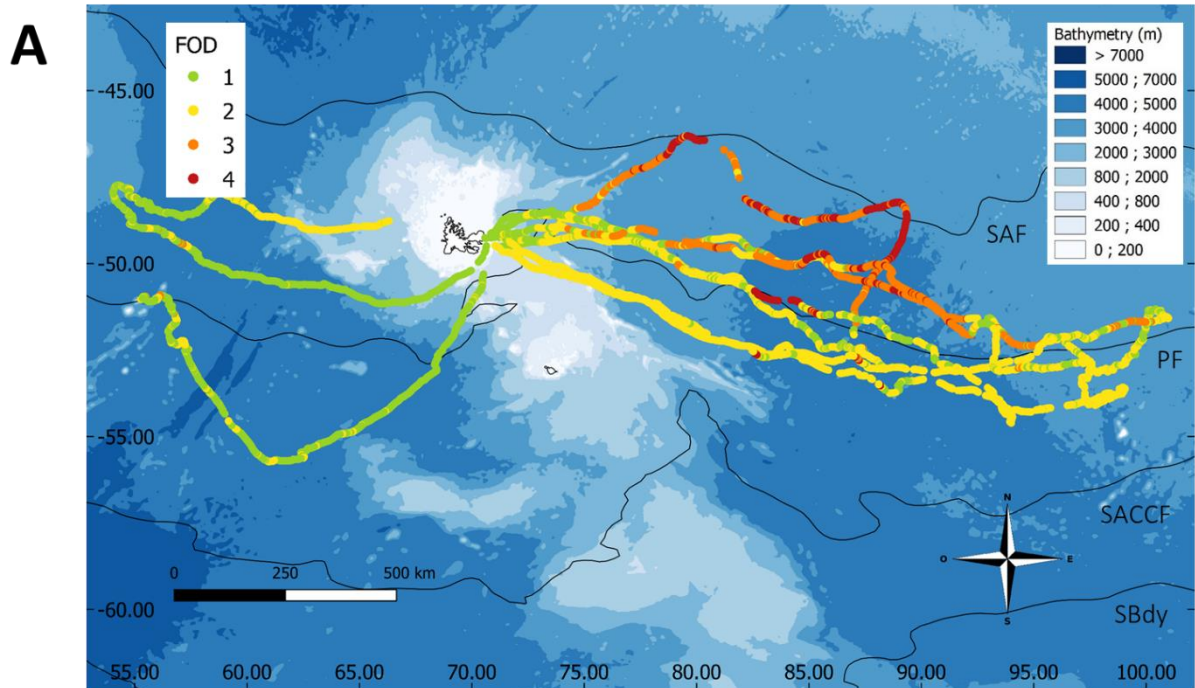
357 variation in salinity (Figure 2). Seals foraging East of Kerguelen visited mainly FOD 2  
 358 (46% of dives) and in comparison performed little feeding activity in the warmer FOD  
 359 1, 3 and 4 (22%, 22% and 11% of dives respectively, Table 2). In contrast, the two  
 360 individuals foraging West of Kerguelen mostly concentrated their foraging activity in  
 361 FOD 1 (79% of dives), the coldest FOD. They performed 21% of dives in FOD 2, and  
 362 never visited FOD 3 and 4 (Table 2).

363 Table 2: Proportion of dives performed in each FOD visited by nine females SES from  
 364 Kerguelen Islands equipped with high-resolution sonar and movement tags between  
 365 2018 and 2020. FOD were identified from in-situ temperature and salinity profiles  
 366 recorded by CTD tags. One GPS sensor and one CTD tag failed to record any data for  
 367 individuals ml18\_293a and ml19\_296a respectively, so FOD could not be determined  
 368 for these individuals.

Seal ID	FOD1	FOD2	FOD3	FOD4
ml18_292a	82	18	0	0
ml18_293a	NA	NA	NA	NA
ml18_294a	8	10	49	33
ml19_295a	36	63	0	1
ml19_295c	41	43	3	13
ml19_296a	NA	NA	NA	NA
ml20_295a	13	61	25	2
ml20_296a	9	52	33	6

ml20_296c	76	23	1	0
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369



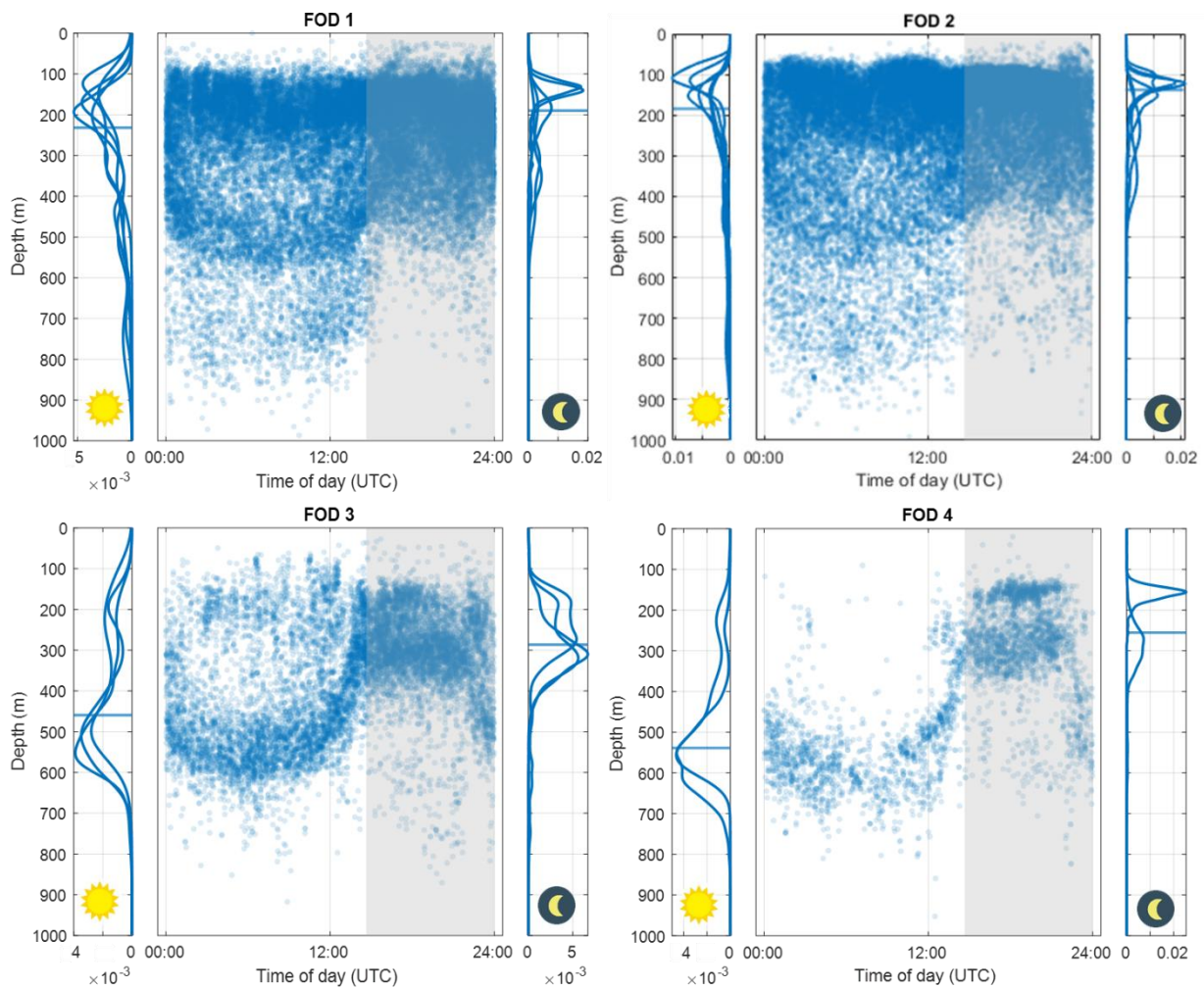
370

371 Figure 2: (A) GPS tracks of seven female Southern SES from Kerguelen Islands

372 equipped with high-resolution sonar and movement tags in 2018 (n = 2), 2019 (n = 2)

373 and 2020 (n = 3). Colours represent FOD encountered by seals, identified from in-situ  
374 temperature and salinity profiles recorded by CTD tags. Black lines indicate the mean  
375 position of the following oceanic fronts: South-Antarctic Front (SAF), Polar Front (PF),  
376 South Antarctic Circumpolar Current Front (SACCF) and Southern Boundary of the  
377 Antarctic Circumpolar Current (SBdy) extracted from Kim et al. (2014). (B) Average  
378 temperature and salinity profiles of the four FOD encountered by seals during their  
379 foraging trips. For each profile, the envelopes are bounded by the first and last quartiles  
380 and thus contain 50% of the profiles.

381 Bouts performed in FOD 3 and 4 were significantly deeper than those performed in  
382 FOD 1 and 2 during both day and night (depth<sub>day</sub> = 296 ± 169 m, 244 ± 165 m, 414 ±  
383 159 m, 508 ± 138 m in FOD 1, 2, 3 and 4 respectively, depth<sub>night</sub> = 224 ± 105 m, 179  
384 ± 98 m, 287 ± 100 m, 254 ± 94 m in FOD 1, 2, 3 and 4 respectively, LMM, P < 0.001,  
385 Figure 3). Difference in day and night bout depths was more pronounced in FOD 3 and  
386 4 (bout depth<sub>day</sub> – bout depth<sub>night</sub> = 99 ± 113 m and 205 ± 98 m respectively) compared  
387 to FOD 1 and 2 (bout depth<sub>day</sub> – bout depth<sub>night</sub> = 60 ± 90 and 42 ± 91 m respectively,  
388 LMM, P < 0.005).



389

390 Figure 3: Depth of bouts over a 24h cycle recorded for the seven female SES equipped  
 391 with sonar and movement tags in Kerguelen Islands from 2018 and 2020, separated  
 392 by FOD visited. Each point represents a bout. The grey background represents  
 393 nighttime. Curves on the left and right of each scatterplot represent the density  
 394 distribution of the bout depth during day and night respectively reconstructed for each  
 395 seal that spent more than 10% in the FOD, with the horizontal line representing the  
 396 median depth.

397 The proportion of evasive prey was significantly higher in FOD 3 and 4 (93.9% and  
 398 90.6% respectively) than in FOD 1 and 2 (75.1 and 77.7% respectively) (GLMM,  $P <$   
 399 0.001, Table 3). Similarly, prey tended to react at a larger distance in FOD 3 and 4 ( $72$   
 400  $\pm 41$  cm and  $74 \pm 44$  cm respectively) than in FOD 1 and 2 ( $65 \pm 38$  cm and  $56 \pm 26$



401 cm respectively) (LMM,  $P < 0.039$ , Table 3). The proportion of flashing prey was  
 402 significantly higher in FOD 1 and 2 (28.5% and 27.9% respectively) than in FOD 3  
 403 (13.7%) (GLMM,  $P < 0.001$ ). Acoustic sizes of prey encountered in FOD 4 were  
 404 significantly greater than those of prey encountered in FOD 1, 2 and 3 ( $7.4 \pm 3.2$  cm,  
 405  $7.2 \pm 3.0$ ,  $7.0 \pm 3.6$  cm and  $8.1 \pm 3.4$  cm for FOD 1, 2, 3 and 4 respectively)  
 406 (Kolmogorov-Smirnov test,  $P = 0.009$ , Table 3). Bouts performed in FOD 3 and 4 were  
 407 significantly longer than those performed in FOD 1 and 2 ( $9.7 \pm 11.6$  s,  $10.3 \pm 12.3$  s,  
 408  $13.4 \pm 14.5$  s,  $13.3 \pm 13.3$  s for FOD 1, 2, 3 and 4 respectively) (LMM,  $P < 0.021$ ,  
 409 Table 3).

410 Table 3: Bout duration, characteristics and behaviour of prey encountered by seven  
 411 female SES equipped with high-resolution movement and sonar tags in Kerguelen  
 412 Islands from 2018 to 2020, according to the FOD visited. Values are mean  $\pm$  sd [1<sup>st</sup> -  
 413 3<sup>rd</sup> quartiles]. Letters in superscript indicate significant differences in prey  
 414 characteristics between FOD (GLMM for proportion of evasive prey, LMM for prey  
 415 reaction distance and bout duration, Kolmogorov-Smirnov test for acoustic size,  $P <$   
 416 0.050).

FOD	Proportion of evasive prey (%)	Prey reaction distance (cm)	Proportion of flashing prey (%)	Acoustic size (cm)	Bout duration (s)
1	75.1 <sup>a</sup>	$65 \pm 38$ <sup>a</sup>	28.5 <sup>a</sup>	$7.4 \pm 3.2$ [5.1 – 9.0] <sup>a</sup>	$9.7 \pm 11.6$ <sup>a</sup>
2	77.7 <sup>a</sup>	$56 \pm 26$ <sup>a</sup>	27.9 <sup>a</sup>	$7.2 \pm 3.0$ [5.1 – 9.0] <sup>a</sup>	$10.3 \pm 12.3$ <sup>b</sup>
3	93.9 <sup>b</sup>	$72 \pm 41$ <sup>b</sup>	13.7 <sup>b</sup>	$7.0 \pm 3.6$ [4.6 – 9.0] <sup>a</sup>	$13.4 \pm 14.5$ <sup>c</sup>

4	90.6 <sup>b</sup>	74 ± 44 <sup>b</sup>	NA	8.1 ± 3.4 [5.9 – 9.8] <sup>b</sup>	13.0 ± 13.3 <sup>d</sup>
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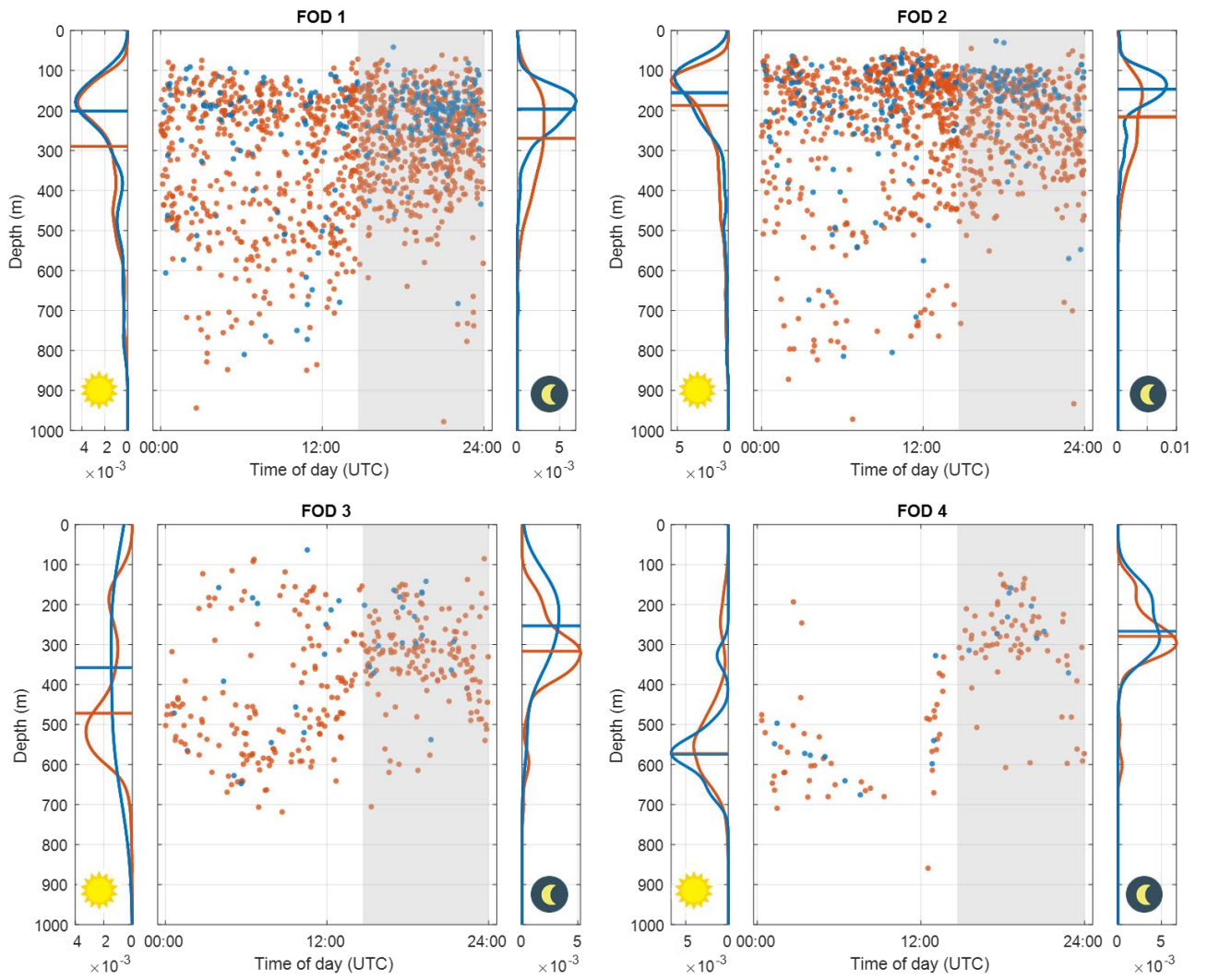
417

418 3.4. Intra-functional oceanographic domain differences in prey  
419 characteristics and distribution

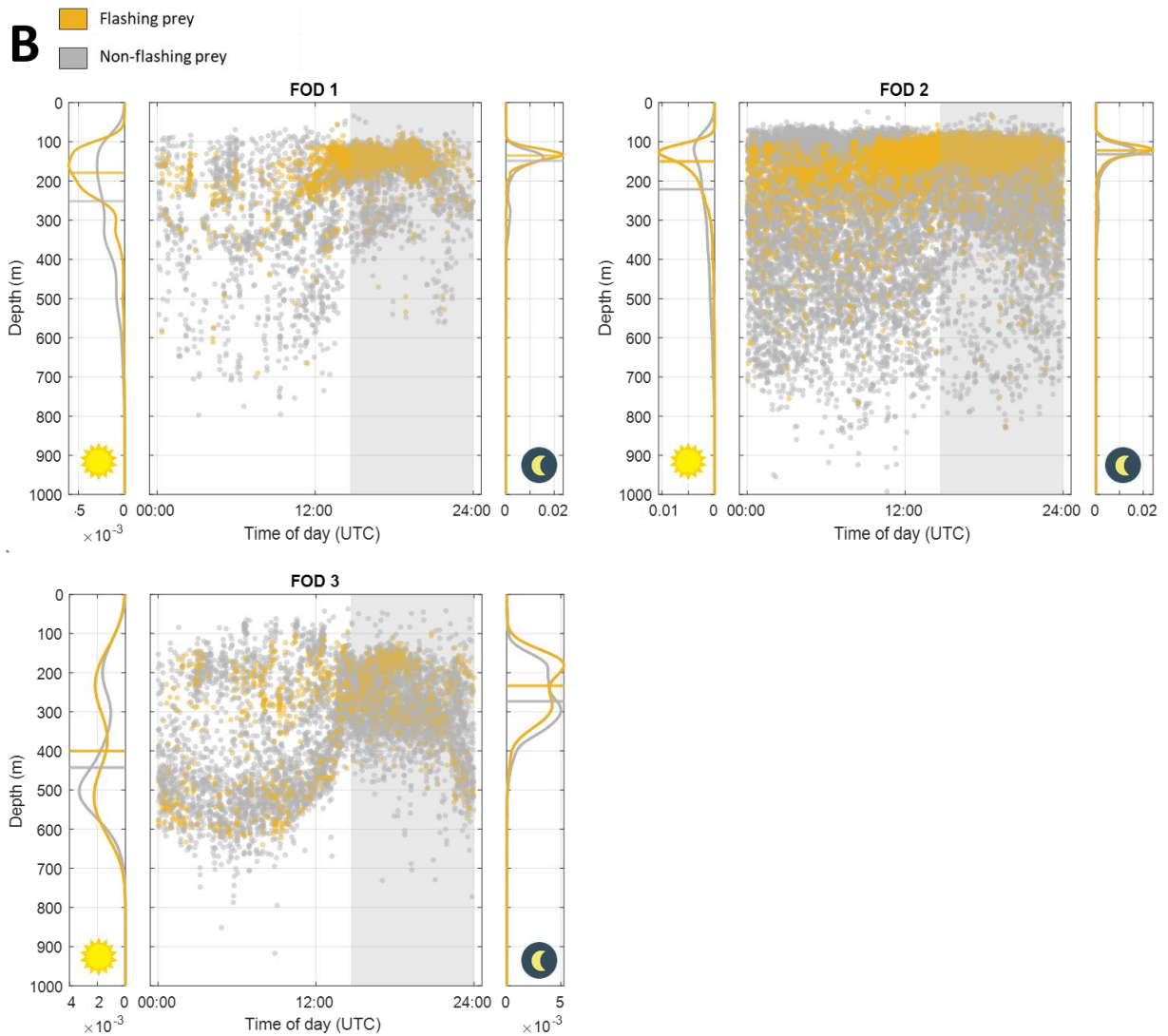
420 In FOD 1, 2 and 3, evasive prey were distributed into two distinct depth layers during  
421 the day, i.e. 100-300 m and 400-600 m, moving up to the sub-surface layers at night  
422 (Figure 4). In FOD 4, the sub-surface layer was not visible during the day and prey  
423 were mostly concentrated in the 500-700 m layer. On the opposite, non-evasive prey  
424 were mostly encountered in sub-surface layers, in depths ranging from 100 to 300  
425 during both day and night, except in FOD 3 and 4. Overall, non-evasive prey were  
426 encountered significantly shallower than evasive ones during both day and night (LMM,  
427  $P < 0.001$ , Figure 4). Similar to non-evasive prey, flashing prey were also mostly  
428 distributed in the sub-surface layers, i.e. 100-300 m during both day and night, except  
429 in FOD 3 and 4 where they were divided into two depth layers during the day, i.e. 100-  
430 300 m and 400-700 m (Figure 4). However, flashing prey were still encountered  
431 significantly shallower than non-flashing ones during both day (LMM,  $P = 0.017$ ) and  
432 night (LMM,  $P = 0.010$ , Figure 4).

**A**

Reactive prey  
Non-reactive prey



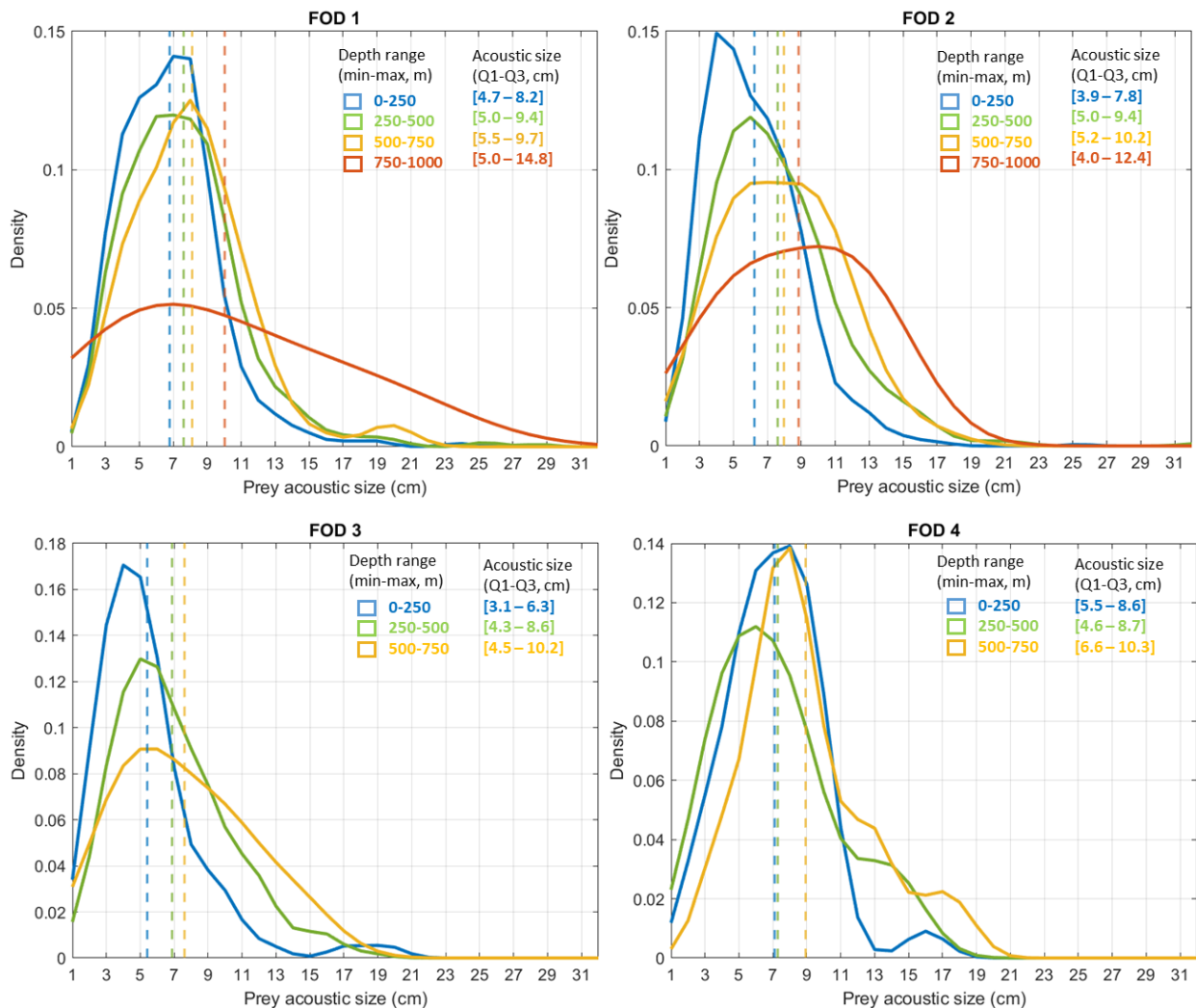
433



434

435 Figure 4: Depth of bouts over a 24h cycle recorded for female SES equipped with sonar  
 436 and movement tags in Kerguelen Islands from 2018 and 2020. Each point represents  
 437 a bout targeting (A) evasive or non-evasive prey (red and blue dots respectively,  $n = 7$   
 438 seals), and (B) flashing or non-flashing prey (yellow and grey dots respectively,  $n = 2$   
 439 seals). The grey background represents nighttime. Curves on the left and right of each  
 440 scatterplots represent the density distribution of the bout depth during day and night  
 441 respectively reconstructed for each seal that spent more than 10% in the FOD, with  
 442 the horizontal line representing the median depth.

443 In all FOD, acoustic size of prey encountered in deeper waters was significantly greater  
 444 than acoustic size of prey encountered in sub-surface layers (Kolmogorov-Smirnov  
 445 test,  $P < 0.009$ , Figure 5).



446  
 447 Figure 5: Prey acoustic size density distributions reconstructed for each depth class  
 448 and for each FOD visited by seven female SES equipped with sonar and movement  
 449 tags between 2018 and 2020 in Kerguelen Islands. The dashed lines represent the  
 450 mean acoustic size calculated for each depth class.

451 In all FOD, bout duration increased with bout depth (LMM,  $P < 0.001$ ): every 100 m,  
 452 bout duration increased by  $1.5 \pm 0.04$  s,  $1.3 \pm 0.04$  s,  $2.3 \pm 0.09$  s, and  $1.0 \pm 0.12$  s for  
 453 FOD 1, 2, 3 and 4 respectively.

454 Bout duration  $FOD_1 = (6.4 \pm 0.6) + (0.015 \pm 0.0004) \cdot \text{depth}$

455 Bout duration  $FOD_2 = (7.0 \pm 0.7) + (0.013 \pm 0.0004) \cdot \text{depth}$

456 Bout duration  $FOD_3 = (4.7 \pm 0.8) + (0.023 \pm 0.0009) \cdot \text{depth}$

457 Bout duration  $FOD_4 = (8.6 \pm 1.2) + (0.010 \pm 0.0012) \cdot \text{depth}$

## 458 4. Discussion

### 459 4.1. A new approach to infer mesopelagic prey distribution via deep-diving 460 predators

461 We deployed on female SES an innovative miniaturised sonar tag that combines active  
462 acoustics with high-resolution movement and bioluminescence sensors to describe  
463 fine-scale characteristics of prey targeted by seals, i.e. their acoustic size, escape  
464 behaviour, bioluminescent behaviour and gregarious behaviour. Sonar tags were  
465 deployed simultaneously with CTD tags to record fine-scale in-situ oceanographic data  
466 during prey encounters, offering a unique opportunity to study prey characteristics and  
467 behaviour simultaneously in relation to oceanographic conditions in a Southern Ocean  
468 deep-diving predator. By deploying these tags on a deep-diving predator that forage  
469 on mesopelagic prey, the SES, we were able to get some insights into mesopelagic  
470 prey distribution and ecology.

### 471 4.2. Insights into mesopelagic prey distribution and habitat

472 All prey were encountered in deep open waters outside the Kerguelen plateau, and  
473 were not associated with particular topographic features. Most prey encounters  
474 occurred in depths ranging from 100 to 800 m, and were characterised by a clear diel  
475 pattern with shallower encounters at night. However, this diel migration behaviour was

476 most noticeable in warmer waters. Female SES are known to target mesopelagic  
477 fishes such as myctophids (Cherel et al., 2008), whose ecology is consistent with our  
478 results (Catul et al., 2011). Prey acoustic size mostly ranged from 3 to 10 cm, which is  
479 close to the main size of myctophids inhabiting Kerguelen waters (Duhamel et al.,  
480 2000; Hulley and Duhamel, 2011), although it is important to remember that acoustic  
481 and actual sizes are not necessarily similar. Indeed, acoustic size is dependent on  
482 target orientation (Burwen et al., 2003), which cannot be controlled for here. However,  
483 when a prey escapes, it will likely be at some point oriented in the axis of the sonar  
484 beam, so measuring the maximum size of the trace of escaping prey should provide a  
485 reliable indication of the prey actual size. Therefore, data collected support the  
486 hypothesis that most targets insonified by the sonar tag during prey capture events  
487 had a body size consistent with myctophids, or more broadly small size mesopelagic  
488 fishes and squids.

489 Even if data recorded by sonar tags do not allow for identifying species targeted by  
490 seals, it provided some precious information about their acoustic size, bioluminescent  
491 behaviour, escape behaviour and gregarious behaviour, allowing us to explore  
492 differences in prey types according to functional oceanographic domains (FOD) visited  
493 by seals. During their foraging trips, seals visited four FOD distributed along an  
494 increasing temperature gradient. FOD 1 and 2 were the coldest, with temperature  
495 below 2 and 2.5°C respectively. These two FOD might correspond to cold waters south  
496 of the Polar Front, characterised by an upper temperature of 2.8°C at 200 m (Park et  
497 al., 1993), with FOD 1 likely influenced by the southern boundary of Southern Antarctic  
498 Circumpolar Current, defined by a temperature of 1.6°C at 200 m (Park et al., 1993).  
499 The Polar Frontal area is characterised by intense mesoscale activity, allowing the  
500 concentration of organic material and therefore a high biological production, so FOD

501 closed to the Polar Front might be particularly productive. In contrast, FOD 3 and 4  
502 were characterised by an upper temperature of 4-5°C and 7°C respectively and  
503 correspond to warmer water north to the Polar Front, and close to the Subantarctic  
504 Front for FOD 4 (Park et al., 1993). As waters North of Kerguelen are known to be less  
505 productive (Godet et al., 2020), FOD 4 is likely characterised by a lower productivity  
506 than other FODs.

507 Trawling and acoustic surveys around Kerguelen Islands showed contrasted  
508 mesopelagic communities between north and south of the Polar Front. *Krefftychthys*  
509 *anderssoni* (1-8 cm) and *Electrona antarctica* (3-10 cm) dominate the myctophid  
510 community south of the Polar Front, while *Electrona carlsbergi* (4-10 cm),  
511 *Gymnoscopelus fraseri* (5-11 cm), *G. bolini* (15-28 cm) and *G. braueri* (4-14 cm) are  
512 more abundant north of the Polar Front (Collins et al., 2008; Duhamel et al., 2000;  
513 Hulley and Duhamel, 2011). The Polar Front is a transition zone between cold Antarctic  
514 waters and warmer subtropical waters (Gordon, 1971). By acting as a boundary  
515 between two different hydrological regions, it constitutes a barrier for many species,  
516 resulting in marked differences in marine communities north and south of the Polar  
517 Front (Koubbi, 1993). Therefore, we would expect to observe differences in prey  
518 behaviour and characteristics between FOD 1-2 (colder waters, south of the Polar  
519 Front) and FOD 3-4 (warmer waters, north of the Polar Front).

520 Prey were slightly larger in FOD 3-4 compared to FOD 1-2, however we expected the  
521 size difference to be more pronounced. Nevertheless, we noticed differences in prey  
522 behaviour depending on the FOD: the proportion of evasive prey was higher in warmer  
523 waters, while the proportion of flashing prey was lower. In addition, diel vertical  
524 migration patterns were more pronounced in warmer waters, suggesting that prey  
525 encountered north and south of the Polar Front are of distinct species, differing in terms



526 of reactivity, bioluminescent behaviour and diel vertical migration behaviour. Acoustic  
527 data recorded by bioluminescence-sonar tags therefore provide novel insights on  
528 differences on mesopelagic prey behaviour according to oceanographic conditions.

529 Moreover, for each given FOD, we observed strong differences in prey acoustic size  
530 and behaviour according to depth. Prey encountered deeper were larger than those  
531 encountered in sub-surface layers no matter the FOD visited. Therefore, prey size and  
532 behaviour seemed to be structured mostly vertically, as observed in previous studies  
533 showing that depth is one of the most important factors in the variability of mesopelagic  
534 communities (Cook et al., 2013; Kenchington et al., 2020; Sutton et al., 2010). Hulley  
535 and Duhamel (2011) reported that within a myctophid species, larger and older  
536 individuals are usually encountered deeper than smaller ones. Therefore, vertical size  
537 structuration observed in all FOD visited by our tagged seals is consistent with previous  
538 findings and is likely to be related with differences in maturity stages between individual  
539 prey and not necessarily due to differences in targeted species.

540 In addition to observing differences in prey size with depth, we also highlighted  
541 differences in prey behaviour along the water column. Bioluminescent prey were  
542 mostly encountered in sub-surface layers during both day and night, while we expected  
543 to observe them in deeper waters (Haddock et al., 2010). Moreover, non-evasive prey  
544 were concentrated to shallow waters during both day and night, while evasive prey  
545 were also encountered in deeper waters. This pattern was observed in all FOD visited  
546 by seals, even if it was more noticeable in colder FOD as few prey were encountered  
547 in sub-surface layers in warmer FOD. Although we would have expected that prey  
548 encountered in deeper and therefore colder waters were less evasive due to a slower  
549 metabolism (Torres and Somero, 1988), we assumed that deep prey, being larger,

550 were more vigilant than smaller/younger individuals encountered in shallower waters  
551 due to an increasing predation risk with prey size (Møller and Erritzøe, 2014).

552 To summarise, prey encountered in colder FOD could mostly belong to Antarctic  
553 species such as *Electrona antarctica* or *Krefftichthys anderssoni*, with either adults *K.*  
554 *anderssoni* or juveniles *E. antarctica* in sub-surface layers during both day and night,  
555 and adult *E. antarctica* exhibiting diel migration being deeper waters during the day,  
556 and going back to the sub-surface layers at night (Duhamel et al., 2000). However, the  
557 fact that the sub-surface layers seemed dominated by small, non-evasive and  
558 bioluminescent prey that did not perform diel vertical migration may suggest that these  
559 prey could be other organisms than myctophids such as small bioluminescent  
560 gelatinous low energy content organisms or euphausiids (Cotté et al., 2022; Trebilco et  
561 al., 2019). In warmer FOD, prey encountered could belong to species associated with  
562 the subtropical waters such as the genus *Gymnoscopelus*, larger and faster swimming  
563 more evasive myctophid species, usually encountered in deeper waters and known to  
564 perform diel vertical migration (Duhamel et al., 2000). However, for the moment, there  
565 is still uncertainties regarding the nature of targets insonified by the sonar so our  
566 interpretations about the potential species targeted by SES must be taken very  
567 cautiously.

#### 568 **4.3. Where to hunt?**

569 Seals concentrated most of their foraging activity in FOD 1 and 2, i.e. south of the Polar  
570 Front. As observed by Field et al. (2004), Guinet et al. (2014) and McMahon et al.  
571 (2019), the southern Polar Frontal zone appears to be a preferred area for seals, as  
572 they performed shallower dives in that area compared to FOD 3 and 4. The Polar Front  
573 is the main foraging area of many species of birds and marine mammals. This area is

574 characterised by intense mesoscale activity, allowing the concentration of organic  
575 material and therefore a high biological production. In particular, the southern Polar  
576 Frontal zone is known to gather 80% of the myctophid biomass of the Southern Ocean  
577 (Lubimova et al., 1987), making this area particularly interesting for SES.

578 Our main hypothesis was that some habitats showed higher prey accessibility and/or  
579 prey quality and were therefore preferred by seals. We found that prey encounters  
580 were significantly deeper in warmer FOD during both day and night. This result is  
581 consistent with observations by Guinet et al. (2014), Biuw et al. (2007) and McIntyre et  
582 al. (2011), showing that bout depth increases with water temperature. Data recorded  
583 during trawling and acoustic surveys revealed a deepening of myctophid community  
584 when getting closer to subtropical waters (Hulley and Duhamel, 2011), suggesting that  
585 prey were less accessible in warmer FOD compared to cold FOD. Light attenuation  
586 plays a major role in defining the depth distribution of mesopelagic organisms (Aksnes  
587 et al., 2017). It has been shown that the deep-scattering layer depth is influenced by  
588 light attenuation, with a deepening of the deep-scattering layer in clearer waters  
589 (Aksnes et al., 2017). In addition, phytoplankton biomass strongly influences the water  
590 transparency and light attenuation (Bracher and Tilzer, 2001; Tilzer et al., 1994).  
591 Subtropical waters in the Southern ocean are known to be less productive with lower  
592 chlorophyll a concentrations than subantarctic waters (Godet et al., 2020). Therefore,  
593 warmer FOD are likely characterised with lower phytoplankton abundance than colder  
594 FOD, which suggests that warmer FOD might be clearer than colder FOD, known to  
595 be more productive (Godet et al., 2020). This might explain the deepening of the  
596 myctophid community observed in warmer FOD, although his hypothesis could not be  
597 tested here.

598 Moreover, in warmer FOD, prey tended to be slightly more evasive with higher flight  
599 initiation distances. A previous study made on the same dataset showed that seals  
600 capturing evasive prey were more likely to initiate energy-costing active chase, while  
601 non-evasive prey could be passively captured (Chevallay et al., 2023). Indeed, we also  
602 observed that bout duration, a proxy for prey capture difficulty (Goulet et al., 2020),  
603 was longer in warmer FOD, suggesting that prey captured in warmer waters induced  
604 longer handling and/or pursuit times. Goulet et al. (submitted) revealed that evasive  
605 prey were associated with a slower improvement in seals' body condition compared to  
606 non-evasive prey by relating body condition gain to prey behaviour in SES. To our  
607 knowledge, the only studies on the energy content of mesopelagic prey around  
608 Kerguelen Islands focus on two or three myctophid species, and have not shown strong  
609 differences in energy content between the species studied (Lea et al., 2002; Van de  
610 Putte et al., 2006). So there likely is a trade-off between prey size (and energy content)  
611 and energy expenditure SES spent to capture them. More species should be studied  
612 to make assumptions on the nutritional value of the various prey encountered by  
613 elephant seals in the different FOD visited. However, differences in prey behaviour and  
614 accessibility between FOD suggest that larger and deeper prey encountered north of  
615 the Polar Front might be less accessible and more difficult to capture, increasing  
616 locomotion costs, which might make these environments less profitable for elephant  
617 seals.

#### 618 **4.4. Limits of the study**

619 This study highlights the usefulness of the bioluminescence-sonar tag to infer  
620 mesopelagic prey distribution and behaviour when deployed on deep-diving predators.  
621 However, the main limitation of animal-borne instruments for environmental sampling  
622 is that sampling is biased by the foraging behaviour of the equipped predator. In

623 particular, it can be difficult to disentangle inter-FOD differences with individual  
624 preferences, as not all seals visit all FOD. However, when looking for each individual  
625 the differences in foraging behaviour between FOD, inter-FOD differences were more  
626 pronounced than the inter-individual differences inside each FOD (see Figure 3),  
627 suggesting that there are actual structural differences between FOD that are not  
628 related to individual preferences. In addition, it is known that seals oversample areas  
629 that favour prey aggregation such as frontal systems (Bailleul et al., 2007; Dragon et  
630 al., 2010; Siegelman et al., 2019) and do not sample deep waters at night because of  
631 the diel migrating pattern of their prey (Slip et al., 1994). Notably, the small size of the  
632 bioluminescence-sonar tag makes it possible to deploy on other diving predator  
633 species such as fur seals or penguins that also feed on mesopelagic prey but in  
634 different vertical/horizontal areas (Bost et al., 2002; Boyd et al., 1991; Charrassin and  
635 Bost, 2001). Deployments on these species could increase spatio-temporal covering  
636 and get a more complete picture of the distribution of mesopelagic prey in the Southern  
637 Ocean. Another limit of this work is related to the use of a functional analysis to  
638 reconstruct temperature-salinity profiles using SES data and to define FOD according  
639 to their similarities in their T-S profiles. This method requires profiles of equal length,  
640 which can be challenging when using data collected by marine predators. We chose  
641 to study profiles only in the first 200 m of the water column as a compromise between  
642 (1) studying a large part of the water column but eliminate a large part of the dives that  
643 do not reach the desired depth, and (2) keeping as many profiles as possible but having  
644 to study a smaller part of the water column. A deeper depth range could help to  
645 describe the mesopelagic prey environment more precisely, however by removing a  
646 large part of the dives that do not reach the desired depth, our clustering would not be  
647 sufficiently representative of the conditions encountered by SES and would therefore

648 not be robust enough. Moreover, by studying the Polar Front variability around  
649 Kerguelen Islands, Pauthenet et al. (2018) showed that most of the variability of the T-  
650 S profiles is contained in the first 200 m, and that variability below 200 m does not  
651 impact the FPCA results, so we believe that our results should be similar with a larger  
652 depth range. Finally, there is still some uncertainties regarding the nature of targets  
653 insonified by the sonar, as acoustic data can be very challenging to interpret.  
654 Subsequently, integrating a camera triggered by acoustic detection to the sonar tag  
655 could help identifying the acoustic targets, and characterising their acoustic signature  
656 to make better use of acoustic data to describe the distribution of mesopelagic prey,  
657 enabling a more precise description of mesopelagic prey characteristics.

#### 658 **4.5. Conclusion**

659 Using a novel multi-sensor approach deployed on a deep-diving predator, the SES, we  
660 explored distribution and ecology of mesopelagic prey targeted by seals and the seals'  
661 foraging behaviour in different oceanographic domains. We highlighted differences in  
662 prey size and behaviour with depth inside each FOD, as well as differences in prey  
663 accessibility and behaviour between FOD, with prey being encountered deeper in  
664 warmer FOD. Climate change leads to a deep-reaching ocean warming, and this  
665 warming is faster in the Southern Ocean compared to the global average (Gille, 2008).  
666 Increase in water temperature can considerably alter organism distributions, e.g.  
667 studies made on several fishes stocks (Nye et al. (2009) on Northeast USA stocks;  
668 Dulvy et al. (2008) on North Sea stocks) revealed a deepening of fishes stocks with  
669 increasing temperature to reach colder waters that are closer to their temperature  
670 ranges (Jorda et al., 2020). Therefore, with ocean warming, prey might become less  
671 accessible, forcing seals to dive deeper, which could lead to significant increase in

672 foraging energy costs and exercise strong selective pressure on larger animals, which  
673 are found to dive deeper (Piot et al., 2023).

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