1 # Spies of the deep: an animal-borne active sonar and

2 # bioluminescence tag to characterise mesopelagic prey size

3 # and behaviour in distinct oceanographic domains

4 Mathilde Chevallay [1] – Tiphaine Jeanniard du Dot [1] – Pauline Goulet [1] – Nadège

5 Fonvieille [2] – Cassandra Craig [1] – Baptiste Picard [1] – Christophe Guinet [1]

6 [1] Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche

7 Scientifique, Villiers-en-Bois, France

8 [2] Mediterranean Institute of Oceanography (MIO), Campus Technologique et

9 Scientifique de Luminy, Marseille, France

10 Corresponding author: Mathilde Chevallay, 405 route de Prissé-la-Charrière 79360

11 Villiers-en-Bois, mathilde.chevallay@outlook.fr

12 **Author contributions**

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

31 **Conflict of interest**

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

Abstract

34 Mesopelagic fish, a central component of marine trophic networks, play a fundamental

35 role in marine ecosystems. However, as they live in highly inaccessible environments,

36 little information is currently available on their ecology, especially on the influence of

37 oceanographic parameters on their distribution. The emergence of biologging

38 technologies has made it possible to use deep-diving predators as bio-samplers of

39 their environment in under-sampled regions. In this work, we deployed an innovative

40 miniaturised sonar tag that combines active acoustics with high-resolution GPS,

41 pressure, movement and light sensors on Southern elephant seals, a deep-diving

42 predator feeding on mesopelagic prey. Seals were also equipped with oceanographic

43 tags, allowing us to explore the functional relationships between oceanographic

44 parameters, distribution and ecology of mesopelagic prey targeted by seals and the

45 seals' foraging behaviour. We highlighted strong vertical differences in prey

46 characteristics and behaviour, with larger, more evasive and less bioluminescent prey

47 in deeper waters. Moreover, prey encountered in warmer waters were found deeper,

48 were more evasive and displayed a more marked diel vertical migration behaviour

49 compared to 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.

1. Introduction

56 Mesopelagic fish 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 of mesopelagic fish

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 micronekton remains poorly known, particularly because they live in highly

66   inaccessible environments. From the perspective of predicting the effects of climate

67   change on marine ecosystems, there is a need to increase our knowledge on the

68   influence of environmental parameters on their distribution.

69   Usual methods to study mesopelagic communities include net sampling and acoustic

70   surveys. Net sampling consists of deploying a net from an oceanographic or fishing

71   vessel in order to collect part of the individuals present in the area with the aim of

72   making an inventory of the species, estimating size of individuals and their biomass.

73   However, net avoidance is commonly observed in pelagic fish, leading to a biased in

74   the species collected (Irigoien et al., 2014; Kaartvedt et al., 2012). Moreover, numerous

75   trawls at different depths are necessary to obtain detailed information on the

76   distribution of species, which may be challenging. In contrast, acoustic surveys

77   describe the fine-scale distribution of organisms in the water column. Most

78   oceanographic vessels are equipped with on-board echosounders that emit

79   successive sound pulses reflected off any object they encounter in the water column

80   (Misund, 1997). The echosounder then receives the returning echo and, depending on

81   the return time, the distance between the echosounder and the object can be

82   estimated. Active acoustics thus provides detailed information on the distribution of

83   organisms but with limited effect on their behaviour. As the distance an acoustic wave

84   can travel in water is inversely proportional to the frequency of that wave,

85   echosounders must emit low frequency waves to sample a large part of the water

86   column. However, low-frequency acoustic waves do not provide detailed echoes of the

87   insonified objects (Misund, 1997). This limits the usefulness of echosounders to obtain

88   fine-scale data on organisms in deeper parts of the water column. Moreover, both

89   acoustic surveys and net samplings require expensive, time-consuming and logistically

90   demanding oceanographic campaigns, that can be highly challenging to set up in

91   remote areas such as polar regions, limiting spatial and temporal coverage.

92   Recent developments of biologging technologies, i.e. devices attached on animals to

93   record information about their behaviour and ecology (Rutz and Hays, 2009), have

94   largely increased our understanding of the ecology of marine predators and their

95   environment (e.g. (Guinet et al., 2014, 2001; Slip et al., 1994; Yoshino et al., 2020)).

96   By integrating high-resolution oceanographic sensors such as temperature, salinity,

97   light or chlorophyll a sensors in tags that can be attached on large deep-diving

98   predators, these predators can be used as bio-samplers of their environment (Fedak,

99   2013; Harcourt et al., 2019; Treasure et al., 2017), making it possible to collect

100   environmental data in under-sampled regions. Investigating the foraging ecology, i.e.

101   at sea distribution, diving behaviour, diet, of marine predators do also provide

102   information on their cryptic and generally poorly known prey (Cherel et al., 2008). In

103   that context and among deep-diving predators, Southern elephant seals (*Mirounga*

104   *leonina,* Linneaus 1758, SES hereafter) are of special interest. SES breed on sub-

105   Antarctic islands and alternate at-sea periods to feed and on-land periods to breed and

106   moult. During their months-long foraging trips, SES travel great distances, up to

107   thousands of kilometres, and perform continuous dives at depths ranging generally

108   from 200 to 1000 m, and up to 2000 m. Therefore, by covering large horizontal and

109   vertical ranges, SES are an ideal species to sample environmental conditions in these

110   remote areas (e.g. (Bailleul et al., 2007; Charrassin et al., 2010; Dragon et al., 2010;

111   Guinet et al., 2014; Tournier et al., 2021). They became a major component in the

112   observation of the Southern Ocean oceanographic conditions (Fedak, 2013). While

113   adult males forage mostly on benthic and benthopelagic prey such as squids, young

114   males and females mainly target mesopelagic prey such as myctophids (Cherel et al.,

115   2008).

116   Deploying high-resolution movement sensors such as accelerometers in addition to

117   oceanographic and GPS sensors on deep-diving predators allows for identifying prey

118   capture attempts (Suzuki et al., 2009; Viviant et al., 2010; Ydesen et al., 2014),

119   providing valuable information on horizontal and vertical distribution of mesopelagic

120   prey targeted by these predators (Guinet et al., 2014). However, fine-scale information

121   on prey, such as their size or behaviour remain challenging to obtain. Miniaturised

122   video cameras can be attached to marine predators foraging in clear and shallow

123   waters (Goldbogen et al. (2017) on blue whales *Balaenoptera musculus*, Heithaus et

124   al. (2002) on tiger sharks *Galeocerdo cuvier*, Papastamatiou et al. (2018) on white-tip

125   sharks *Carcharhinus longimanus*, Semmens et al. (2019) on white sharks

126   *Carcharodon carcharias*). However, SES often forage in the aphotic zone, which

127   requires a light-source to illuminate the scene and capture exploitable images, leading

128   to an increased power consumption of the tag. In addition, using a light source in these

129   deep waters can significantly alter both predator and prey behaviours (Geoffroy et al.,

130   2021; Rooper et al., 2015; Ryer et al., 2009), limiting the usefulness of video cameras

131   to collect meaningful data about SES' prey characteristics and behaviour. Furthermore,

132   recording duration is limited to a few hours, over foraging which can last several

133   months, providing short, but important, glimpse on the prey and foraging behaviour of

134   those species. Very recently, an innovative miniaturised sonar tag has enabled a step

135   forward in the study of fine-scale biotic environment in cryptic marine predators. This

136   state-of-the-art tag, inspired by a toothed whale echolocation system, uses a high-click

137   rate narrow, forward directed beam that can insonify prey at a distance up to 6 m in

138   front of the animal. Data recorded by this tag provide information on prey aggregation

6

139   type, escape behaviour and acoustic size without altering either predator or prey

140   behaviour (Goulet et al., 2019). A more recent version of the sonar tag also includes a

141   light sensor specifically developed to study bioluminescent behaviour of prey (Goulet

142   et al., 2020), offering a unique opportunity to accurately describe behaviour and

143   characteristics of prey targeted by cryptic marine predators (Chevallay et al., in

144   revision).

145   In this context, the aim of this study was to provide a better understanding of the

146   distribution and habitat of mesopelagic prey in the Southern Ocean. Using an

147   innovative method to classify functional oceanographic domains (FOD hereafter)

148   according to their temperature and salinity profiles recorded by conductivity-

149   temperature-depth (CTD) tags (Fonvieille et al., in review; Pauthenet et al., 2017;

150   Tournier et al., 2021) deployed simultaneously with sonar tags on female SES, we

151   aimed at exploring the functional relationships between oceanographic parameters,

152   distribution and ecology of mesopelagic prey targeted by seals and the seals' foraging

153   behaviour. Previous studies showed that seals visit different areas with contrasted

154   oceanographic conditions during their foraging trips (Bailleul et al., 2007; Biuw et al.,

155   2007) and that seals targeting distinct FOD differed in their foraging efficiency (Guinet

156   et al., 2014; Richard et al., 2016). Therefore, we predicted that these contrasted

157   habitats would be home to prey with diverse characteristics and behaviour, and that

158   some habitats favour prey accessibility and/or prey quality (i.e. larger or less evasive

159   prey). Specifically, we hypothesised that prey tend to be more evasive in warmer FOD

160   but also less accessible, as suggested by Guinet et al. (2014) and Richard et al. (2016).

7

2. Material and methods

2.1. Device deployments and data collection

Data were collected on 9 post-breeding female Southern elephant seals in October 2018 (n = 3), October 2019 (n = 3) and October 2020 (n = 3), in Kerguelen Islands (49°20'S – 70°26'E). Females were captured with a canvas head-bag, anaesthetized with a 1:1 combination of Tiletamine and Zolazepam (Zoletil 100 – 0.7 to 0.8 ml/100 kg) either injected intravenously (McMahon et al., 2000) or using a deported intramuscular injection system. Females were measured to the nearest centimetre and weighted to the nearest kilogram. They were equipped with a neck-mounted Argos tag (SPOT-293 Wildlife Computers, 72x54x24 mm, 119 g in air), a back-mounted CTD tag (SMRU-SRDL, 115x100x40 mm, 680 g in air) and either a head-mounted DTAG-4 sonar tag (n = 7, 95x55x37 mm, 200 g in air, see Goulet et al. (2019) for further details on the device) or a DTAG-4 sonar-light tag (n = 2, 92x69x37 mm, 250 g in air). Tags were glued to the fur using quick-setting epoxy glue (Araldite AW 2101, Ciba). CTD tags recorded conductivity, temperature and depth at 0.5 Hz. Sonar and sonar-light tags were programmed to sample GPS position (up to every minute at surface), tri-axial acceleration (200 Hz), tri-axial magnetometer (50 Hz) and pressure (50 Hz). Sonar-light tags also integrated a light sensor specifically designed to sample bioluminescence events with a sampling frequency of 50 Hz (Goulet et al., 2020). The active sonar within the tags recorded acoustic backscatter returning from 10 μs pings with a centre frequency of 1.5 MHz, at a 25 Hz ping rate for 2018 and 2019 deployments and 12.5 Hz for 2020 deployments. The active sonar operated with a 3.4° aperture beam width and a 6 m range (Goulet et al., 2019). Sonar and sonar-light tags were set to record data one day out of two to increase recording duration. Tags were recovered in late December to January when females returned to shore to moult using

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186 the same capture and sedation methods. All experiments were conducted under the

187 ethical regulation approval of the French Ethical Committee for Animal

188 Experimentations (2019070612143224 (#21375)) and the Committee for Polar

189 Environment.

190   2.2.   Foraging behaviour

191 Sonar, movement and location data recorded by the sonar tags were analysed using

192 custom-written codes and functions from www.animaltags.org in MATLAB version

193 2022b (The MathWorks, 2022). Statistical analyses were conducted in R software

194 version 3.5.1 (R Core Team, 2018). GPS tracks were plotted in a map using QGIS

195 version 3.10 (QGIS Development Team, 2019). Diving behaviour was assessed by

196 using pressure data recorded by the sonar tags. Seals were considered as diving when

197 depth exceeded 20 m.

198   2.3.   Prey capture attempt identification

199 Prey capture attempts (PrCAs hereafter) were detected from the 200 Hz tri-axial

200 acceleration data recorded by the sonar tags, by computing the norm of the differential

201 of the tri-axial acceleration (norm-jerk hereafter), as described in Goulet et al.

202 (submitted). Spikes in the norm-jerk higher than 400 m.s^{-2} were classified as PrCAs

203 (Goulet et al., submitted). As prey may be encountered in patches or may elude

204 capture, leading to a bout structure in prey strikes, strikes occurring less than 15 s from

205 the previous strike were grouped in the same bout as described by Goulet et al.

206 (submitted).

207   2.4.   Functional oceanographic domain identification

208   Functional oceanographic domains (FOD hereafter) were classified according to their

209   similarities in their temperature and salinity profiles, following the method described in

210   (Fonvieille et al., in review). We first generated temperature and salinity profiles (TS)

211   on a constant vertical grid from 20 to 200 m for each dive using temperature and salinity

212   data collected by the CTD tags. This depth range was chosen to maximise temporal

213   coverage especially at night when seals perform shallower dives (Tournier et al., 2021).

214   We then fitted B-splines to the profiles with 20 coefficients estimated by polynomial

215   regression (R package "fda", (Ramsay and Silverman, 2005)). A bivariate functional

216   principal component analysis (FPCA, R package "fda") was applied on the resulting

217   coefficients of the decomposition to extract principal modes of variability in the curves

218   shapes (see Pauthenet et al. (2017) and Nerini et al. (2022) for more details). Finally,

219   a model-based clustering (Bouveyron et al., 2019) was applied on the first principal

220   components of the FPCA to gather TS profiles sharing similar thermohaline vertical

221   structure (R package "mclust", (Scrucca et al., 2016)). The appropriate number of

222   clusters was defined using the Bayesian Information Criterion (Schwarz, 1978) and the

223   Integrated Completed Likelihood (Biernacki et al., 2000), as described in Fonvieille et

224   al. (in review). The resulting clusters was considered as representing different FOD

225   and were plotted along the track of SES.

226   2.5.   Prey characteristics and behaviour

227   2.5.1. Sonar data analysis

228   Sonar data recorded during bouts were displayed as echograms, showing the time on

229   the horizontal axis and the distance from the sonar tag on the vertical axis, extending

230   from 10 s before the bout start time to 2 s after the bout end time (Goulet et al.,

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231 submitted). Because of the large number of bouts detected (ranging from 4595 to

232 12039 per animal), only a random subsample of 5 to 10% of bouts performed during

233 acoustic data recordings were analysed. Different variables describing predator-prey

234 interactions were extracted manually from echograms following the method described

235 by Goulet et al. (submitted): (1) number of prey, (2) prey escape behaviour, (3) prey

236 acoustic size. (1) The number of prey was defined as the maximum number of

237 independent echo traces within a same ping (Jones et al., 2008). It was scored as one,

238 two or more than two, i.e. a school of prey. (2) Prey escape behaviour was identified

239 from the closing speed between predator and prey, which will vary in case of prey

240 escape event, resulting in a change in the slope of the prey echo trace (Goulet et al.,

241 2019; Vance et al., 2021). (3) Prey acoustic size was estimated from the -20 dB echo

242 pulse width measured on the widest part of the prey trace on evasive prey only to get

243 an acoustic size estimate as close as possible to the prey length (Burwen et al., 2003).

244   2.5.2. Bioluminescence data analysis

245 Bioluminescent flashes were defined as short high intensity spikes in the 50 Hz light

246 data recorded by the sonar-light tags decimated at a 5 Hz sampling rate. Spikes in the

247 data higher than 0.07 (arbitrary unit) were classified as flashes (Goulet et al., 2020).

248 Flashes detected within less than 5 s of each other were considered coming from the

249 same bioluminescence event (Goulet et al., 2020). If a bioluminescence event started

250 between 5 s before and 5 s after the bout, it was considered associated with the bout.

251 Bioluminescence events may consist of a series of short flashes, so the 5 Hz data may

252 not have sufficient resolution to accurately describe them. Therefore, we used 50 Hz

253 light data recorded during bioluminescence events to calculate the number of peaks in

254 the light signal as well as the intensity and duration of each peak.

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2.6. Statistical analyses

For the following analyses, only data recorded on seals equipped with sonar-light tags were used for the comparisons between flashing and non-flashing prey, while comparisons between evasive and non-evasive prey were made using data recorded by all the sonar-tagged seals. For all subsequent models, assumptions were checked and any deviation from them were corrected in the models.

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

Prey accessibility, using the depth of bout as its proxy (Boyd et al., 2015; Jouma'a et al., 2016) was compared between FOD using LMM (R package nlme, (Pinheiro et al., 2017)) with dive depth as response variable, FOD as fixed effect and seals' individual identities as a random effect during both day and night. To test for differences in prey behaviour according to FOD, the proportion of evasive versus non-evasive prey and flashing versus non-flashing prey was compared between FOD using generalised linear mixed models with binomial distribution (GLMM hereafter, R package lme4, (Bates et al., 2015)). We used the proportion of each prey type as a response variable, FOD as fixed effect and seals' individual identities as a random effect. As the two seals equipped with sonar-light tag almost never visited FOD4, we did not compute the proportion of flashing prey in this FOD. Prey flight initiation distances (m) were compared between FOD using LMM with flight initiation distance as response variable, FOD as fixed effect and seals' individual identifies as a random effect. Bout duration (s), a proxy for prey capture difficulty, or an indication of multi-prey capture (Goulet, 2020), was compared between FOD using LMM with bout duration as a response variable, FOD as fixed effect and seals' individual identities as a random effect. Finally, distribution of prey acoustic size was reconstructed for each FOD and were compared

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280   using a pairwise Kolmogorov-Smirnov test with Bonferroni correction for multiple

281   testing.

282   2.6.2. Intra-functional oceanographic domain differences in prey characteristics

283   and distribution

284   Inside each FOD, difference in depths at which prey were encountered between

285   evasive and non-evasive prey and between flashing and non-flashing prey were

286   compared using prey encounter depth as response variable, prey type (evasive vs.

287   non-evasive prey, flashing vs. non-flashing prey) as fixed effect and seals' individual

288   identities as a random effect. To test the hypothesis that prey size varies with depth,

289   prey acoustic size distributions were reconstructed for depth classes every 200 m, from

290   20 to 1000 m, and were compared using Kolmogorov-Smirnov test with Bonferroni

291   correction for multiple testing inside each FOD. Finally, the relationship between bout

292   duration and bout depth was assessed for each FOD using a LMM with bout duration

293   as response variable, bout depth as fixed effect and seals' individual identifies as a

294   random effect.

3. Results

3.1.   Foraging behaviour and targeted prey

297   Tags recorded data during 29-79 days (Table 1). One GPS sensor and one CTD tag

298   failed to record any data on individual ml18_293a and individual ml19_296a

299   respectively so data recorded from these individuals were not used for spatial

300   analyses. Over that period, seals performed 69 ± 7 (mean ± sd) dives per day (range

301   57-79 dives per day), and 511 ± 53 bouts/day (range 443-610 bouts/day). Seals

302   performed dives 418 ± 93 m deep for 19 ± 3 min. A diel diving pattern was observed

303   for almost all individuals, with deeper and longer dives performed during the day (456

304   ± 96 m, 21 ± 4 min) than during the night (331 ± 75 m, 16 ± 2 min, LMM, P < 0.001).

305   Seals almost exclusively targeted single prey (99% of the targeted prey) while schools

306   of prey represented only 1% of the targeted prey. Among single prey, 81% were

307   evasive. For the two individuals equipped with sonar-light tags, flashing prey

308   represented 24 and 29% of their targeted prey respectively. Prey acoustic size mainly

309   distributed from 5.1 to 9.0 cm (1st and 3rd quartiles, Q1-Q3 hereafter), with a range of

310   1.2-32.8 cm.

311   Table 1: Summary of field deployments: length (cm) and weight (kg), number of days

312   of recordings, number of recorded dives and bouts of female SES from Kerguelen

313   Islands equipped with either sonar or sonar-light tag during their post-breeding foraging

314   trip. Seal ID comprises the two first letters of the Latin species binomial followed by the

315   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

316

317 ## 3.2. Foraging area

318 All seals but two travelled east of the Kerguelen Islands (Figure 1). The two other seals

319 travelled west. They concentrated their foraging activity at a mean distance from the

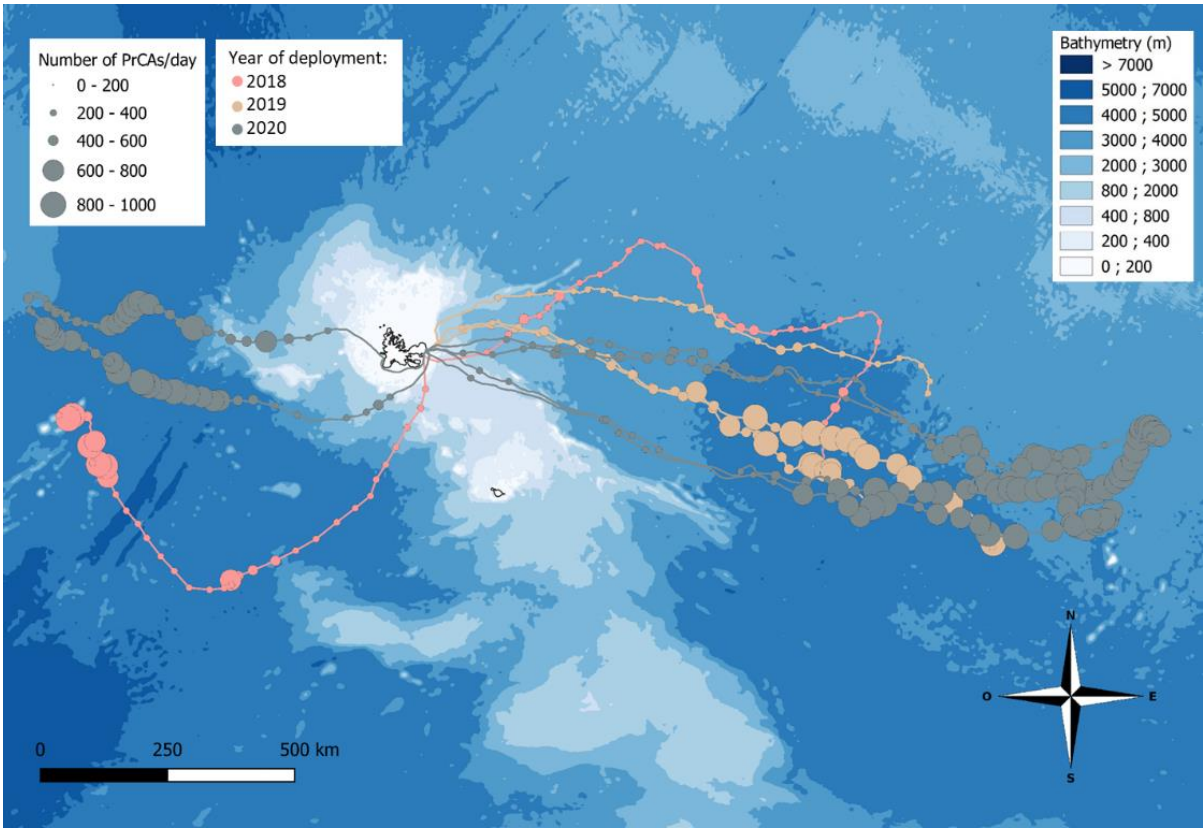320 shore of 1170 ± 539 km (Q1-Q3: 789-1663 km, Figure 1).

321

322 Figure 1: GPS tracks of eight female SES from Kerguelen Islands equipped with high-

323 resolution sonar and movement tags in 2018 (n = 2, in pink), 2019 (n = 3, in beige) and

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324   2020 (n = 3, in grey) during their post-breeding foraging trips (November-January).

325   Each point represents one day, with the size of the point being proportional to the

326   number of bouts performed that day. For 6 females, the tags stopped recording before

327   the end of the foraging trip.

328   3.3.   Inter-functional   oceanographic   domain   differences   in   prey

329   characteristics and distribution

330   During their foraging trips, seals encountered four FOD that we identified from *in-situ*

331   temperature and salinity profiles recorded by CTD tags (Figure 2). These FOD were

332   distributed along an increasing temperature gradient from FOD 1 to FOD 4, with little

333   variation in salinity (Figure 2). Seals foraging East of Kerguelen visited mainly FOD 2

334   (46% of dives) and in comparison performed little feeding activity in the warmer FOD

335   1, 3 and 4 (22%, 22% and 11% of dives respectively, Table 2). In contrast, the two

336   individuals foraging West of Kerguelen mostly concentrated their foraging activity in

337   FOD 1 (79% of dives), the coldest FOD. They performed 21% of dives in FOD 2, and

338   never visited FOD 3 and 4 (Table 2).

339   Table 2: Proportion of dives performed in each FOD visited by seven females SES

340   from Kerguelen Islands equipped with high-resolution sonar and movement tags

341   between 2018 and 2020. FOD were identified from in-situ temperature and salinity

342   profiles recorded by CTD tags.

Seal ID	FOD1	FOD2	FOD3	FOD4
ml18_292a	82	18	0	0
ml18_293a	NA	NA	NA	NA

16

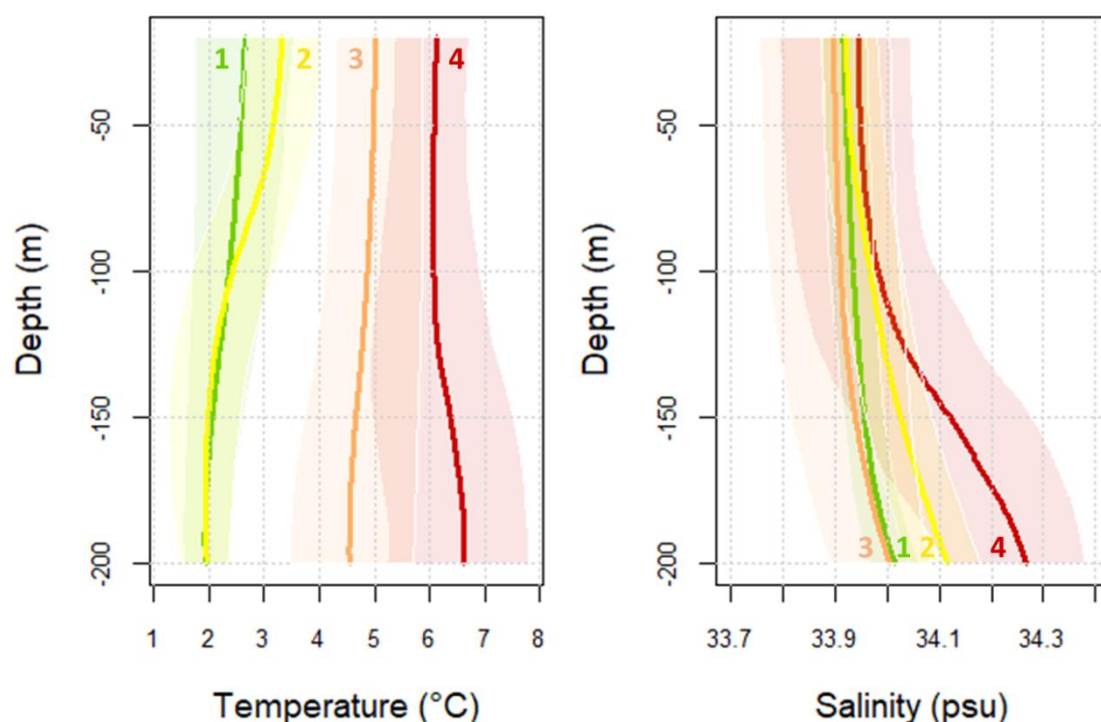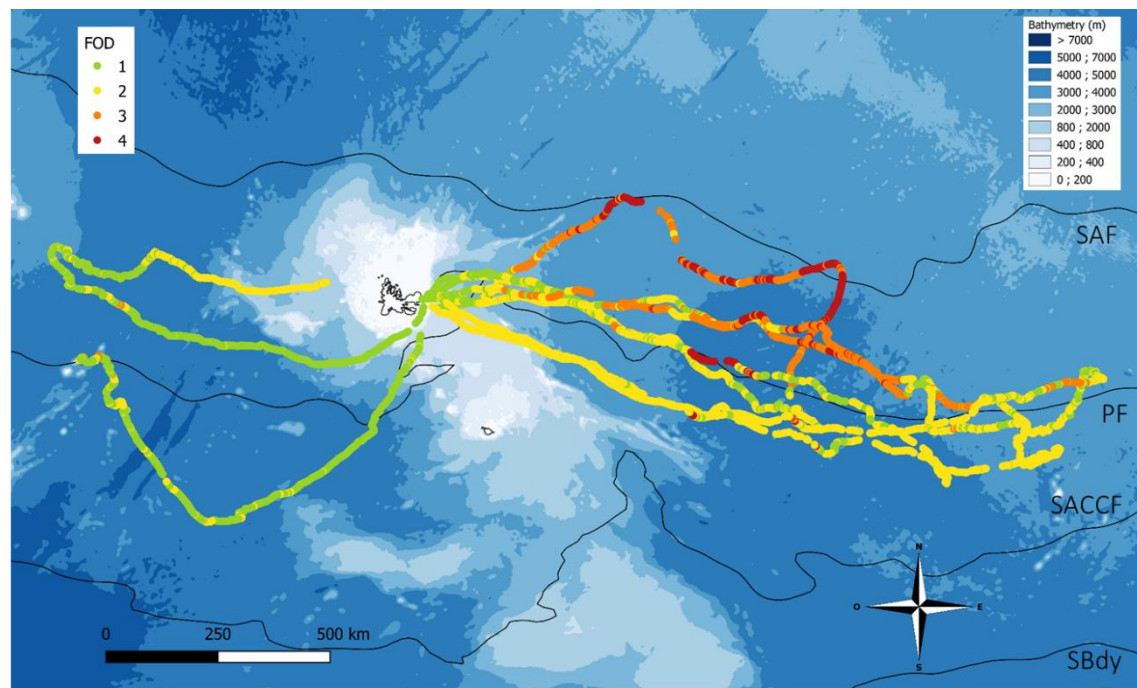|				
ml18_294a	8	10	49	33
ml19_295a	36	63	0	1
ml19_295c	41	43	3	13
ml19_296a	NA	NA	NA	NA
ml20_295a	13	61	25	2
ml20_296a	9	52	33	6
ml20_296c	76	23	1	0

343

Figure 2: (A) GPS tracks of seven female Southern SES from Kerguelen Islands equipped with high-resolution sonar and movement tags in 2018 (n = 2), 2019 (n = 2) and 2020 (n = 3). Colours represent FOD encountered by seals, identified from in-situ temperature and salinity profiles recorded by CTD tags. Black lines indicate the mean position of the following oceanic fronts: South-Antarctic Front (SAF), Polar Front (PF),

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350   South Antarctic Circumpolar Current Front (SACCF) and Southern Boundary of the

351   Antarctic Circumpolar Current (SBdy) extracted from Kim et al. (2014). (B) Average

352   temperature and salinity profiles of the four FOD encountered by seals during their

353   foraging trips. For each profile, the envelopes are bounded by the first and last quartiles

354   and thus contain 50% of the profiles.

355   Bouts performed in FOD 4 were significantly deeper than those performed in FOD 1,

356   2 and 3 during both day and night (depth $_{day}$ = 296 ± 169 m, 244 ± 165 m, 414 ± 159

357   m, 508 ± 138 m in FOD 1, 2, 3 and 4 respectively, depth $_{night}$ = 224 ± 105 m, 179 ± 98

358   m, 287 ± 100 m, 254 ± 94 m in FOD 1, 2, 3 and 4 respectively, LMM, $P < 0.001$, Figure

359   3). Moreover, difference in day and night bout depths was more pronounced in FOD 3

360   and 4 (bout depth $_{day}$ − bout depth $_{night}$ = 99 ± 113 m and 205 ± 98 m respectively)

361   compared to FOD 1 and 2 (bout depth $_{day}$ − bout depth $_{night}$ = 60 ± 90 and 42 ± 91 m

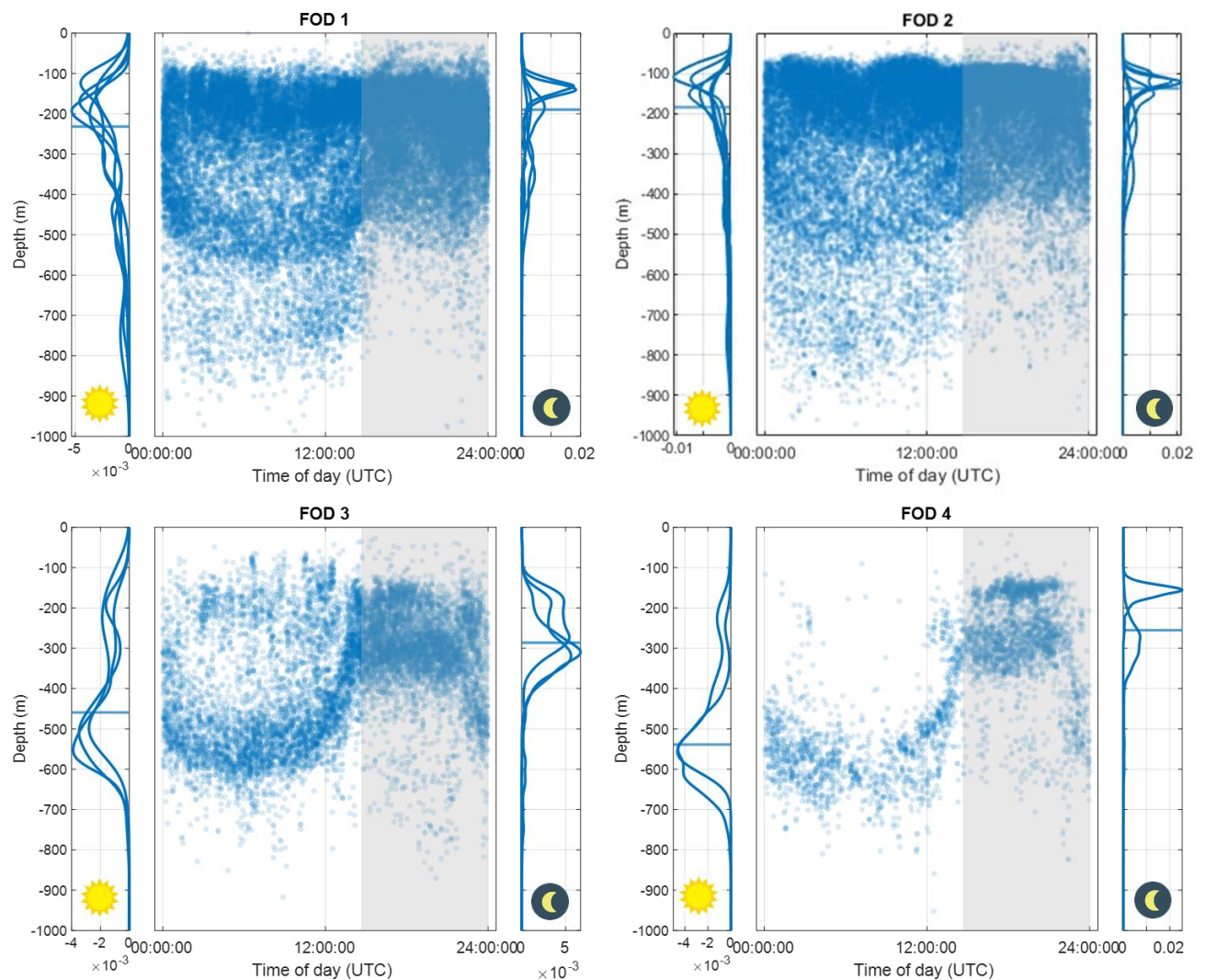362   respectively, LMM, $P < 0.005$).

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

The proportion of evasive prey was significantly higher in FOD 3 and 4 (93.9% and 90.6% respectively) than in FOD 1 and 2 (75.1 and 77.7% respectively) (GLMM, $P < 0.001$, Table 3). Similarly, prey tended to react at a larger distance in FOD 3 and 4 (72

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374   ± 41 cm and 74 ± 44 cm respectively) than in FOD 1 and 2 (65 ± 38 cm and 56 ± 26

375   cm respectively) (LMM, P < 0.039, Table 3). The proportion of flashing prey was

376   significantly higher in FOD 1 and 2 (28.5% and 27.9% respectively) than in FOD 3

377   (13.7%) (GLMM, P < 0.001). Acoustic sizes of prey encountered in FOD 4 were

378   significantly greater than those of prey encountered in FOD 1, 2 and 3 (Kolmogorov-

379   Smirnov test, P = 0.009, Table 3). Bouts performed in FOD 3 and 4 were significantly

380   longer than those performed in FOD 1 and 2 (LMM, P < 0.021, Table 3).

381   Table 3: Bout duration, characteristics and behaviour of prey encountered by seven

382   female SES equipped with high-resolution movement and sonar tags in Kerguelen

383   Islands from 2018 to 2020, according to the FOD visited. Values are mean ± sd [1st -

384   3rd quartiles]. Letters in superscript indicate significant differences in prey

385   characteristics between FOD (GLMM for proportion of evasive prey, LMM for prey

386   reaction distance and bout duration, Kolmogorov-Smirnov test for acoustic size, P <

387   0.050).

FOD	Proportion of evasive prey (%)	Prey reaction distance (cm)	Proportion of flashing prey (%)	Acoustic size (cm)	Bout duration (s)
1	75.1 [a]	65 ± 38 [a]	28.5 [a]	7.4 ± 3.2 [5.1 – 9.0] [a]	9.7 ± 11.6 [a]
2	77.7 [a]	56 ± 26 [a]	27.9 [a]	7.2 ± 3.0 [5.1 – 9.0] [a]	10.3 ± 12.3 [b]
3	93.9 [b]	72 ± 41 [b]	13.7 [b]	7.0 ± 3.6 [4.6 – 9.0] [a]	13.4 ± 14.5 [c]
4	90.6 [b]	74 ± 44 [b]	NA	8.1 ± 3.4 [5.9 – 9.8] [b]	13.0 ± 13.3 [d]

388   3.4.   Intra-functional oceanographic domain differences in prey

389   characteristics and distribution

390   In FOD 1, 2 and 3, evasive prey were distributed into two distinct depth layers during

391   the day, i.e. 100-300 m and 400-600 m, moving up to the sub-surface layers at night

392   (Figure 4). In FOD 4, the sub-surface layer was not visible during the day and prey

393   were mostly concentrated in the 500-700 m layer. On the opposite, non-evasive prey

394   were mostly encountered in sub-surface layers, in depths ranging from 100 to 300

395   during both day and night, except in FOD 3 and 4. Overall, non-evasive prey were

396   encountered significantly shallower than evasive ones during both day and night (LMM,

397    $P < 0.001$, Figure 4). Similar to non-evasive prey, flashing prey were also mostly

398   distributed in the sub-surface layers, i.e. 100-300 m during both day and night, except

399   in FOD 3 and 4 where they were divided into two depth layers during the day, i.e. 100-

400   300 m and 400-700 m (Figure 4). However, flashing prey were still encountered

401   significantly shallower than non-flashing ones during both day (LMM, $P = 0.017$) and

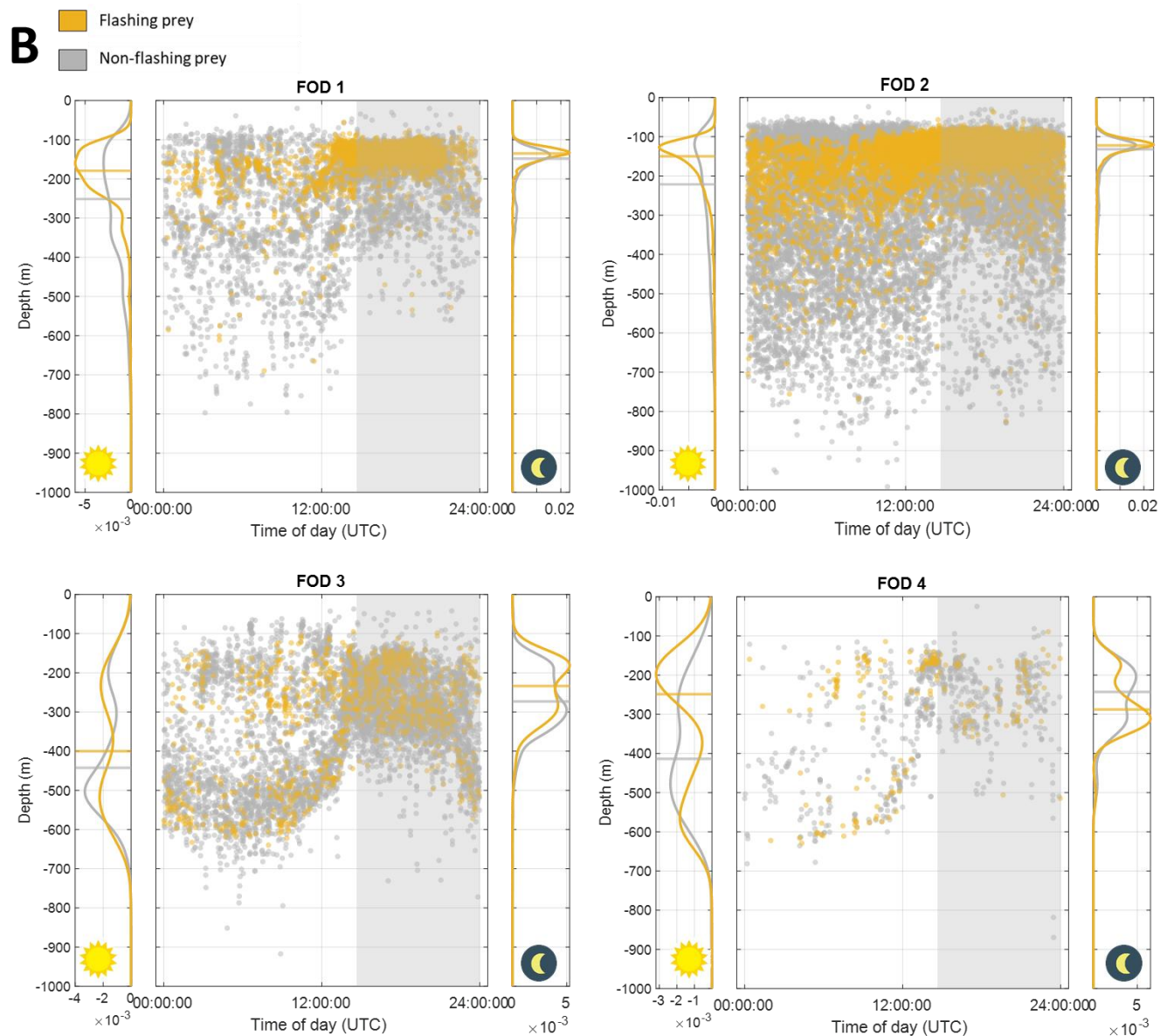402   night (LMM, $P = 0.010$, Figure 4).
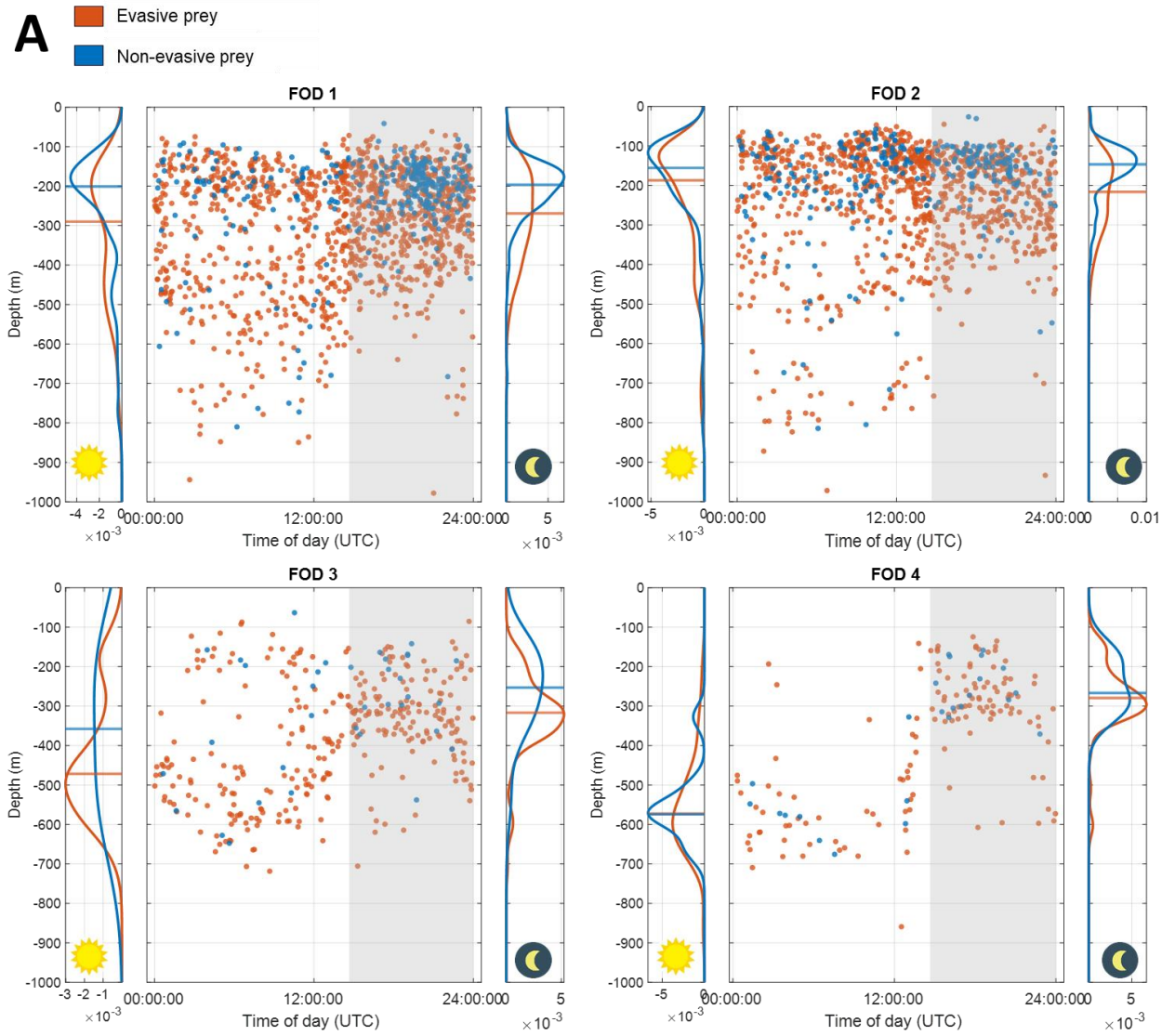
403

Figure 4: Depth of bouts over a 24h cycle recorded for female SES equipped with sonar and movement tags in Kerguelen Islands from 2018 and 2020. Each point represents a bout targeting (A) evasive or non-evasive prey (red and blue dots respectively, n = 6 seals), and (B) flashing or non-flashing prey (yellow and grey dots respectively, n = 2 seals). The grey background represents nighttime. Curves on the left and right of each scatterplots represent the density distribution of the bout depth during day and night respectively, with the horizontal line representing the median depth.

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412 In all FOD, acoustic size of prey encountered in deeper waters was significantly greater

413 than acoustic size of prey encountered in sub-surface layers (Kolmogorov-Smirnov
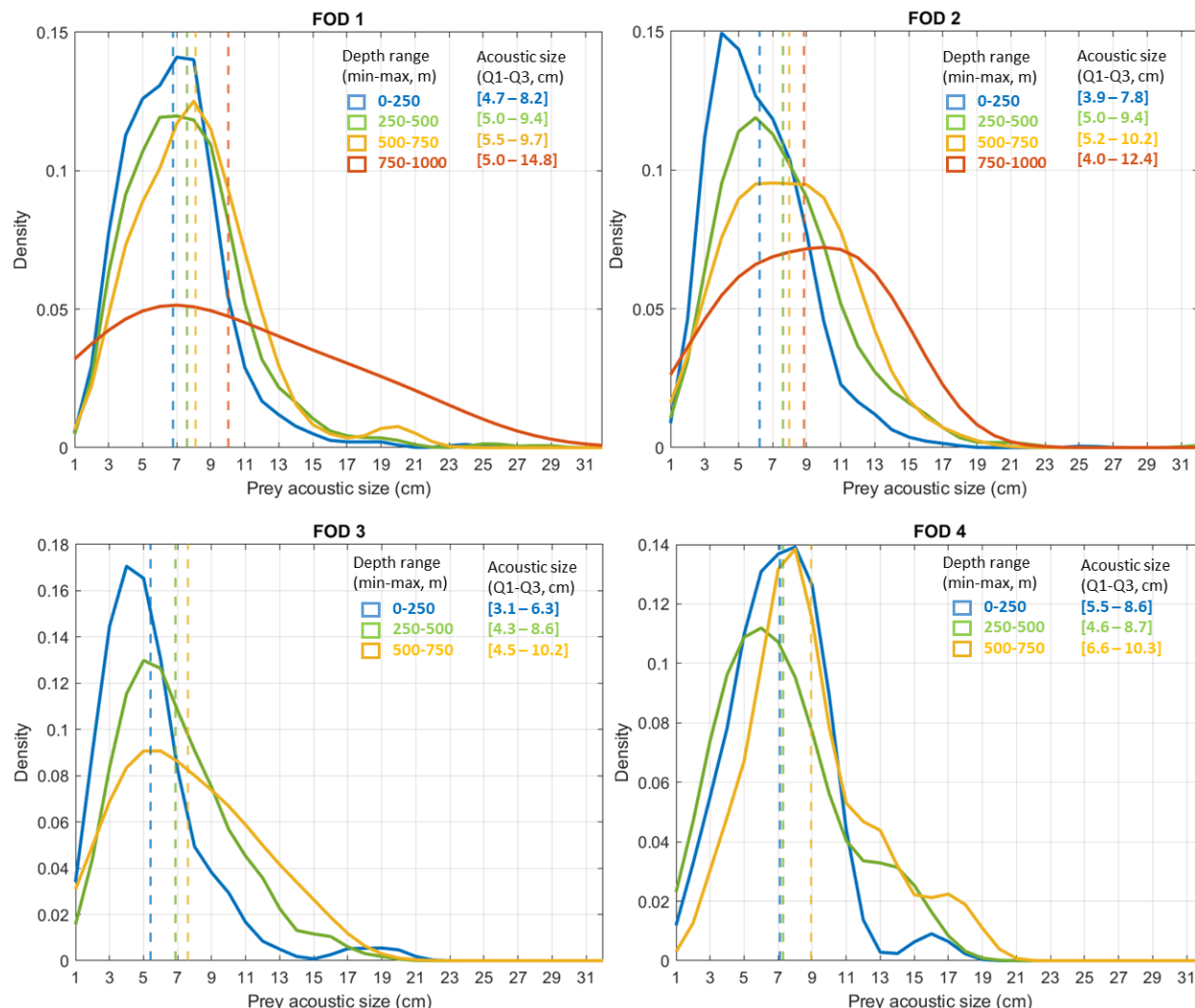
414 test, $P < 0.009$, Figure 5).

415

416 Figure 5: Prey acoustic size density distributions reconstructed for each depth class

417 and for each FOD visited by seven female SES equipped with sonar and movement

418 tags between 2018 and 2020 in Kerguelen Islands. The dashed lines represent the

419 mean acoustic size calculated for each depth class.

420 In all FOD, bout duration increased with bout depth (LMM, $P < 0.001$): every 100 m,

421 bout duration increased by 1.5 ± 0.04 s, 1.3 ± 0.04 s, 2.3 ± 0.09 s, and 1.0 ± 0.12 s for

422 FOD 1, 2, 3 and 4 respectively.

25

423    $\text{Bout duration}_{\text{FOD 1}} = (6.4 \pm 0.6) + (0.015 \pm 0.0004) \cdot \text{depth}$

424    $\text{Bout duration}_{\text{FOD 2}} = (7.0 \pm 0.7) + (0.013 \pm 0.0004) \cdot \text{depth}$

425    $\text{Bout duration}_{\text{FOD 3}} = (4.7 \pm 0.8) + (0.023 \pm 0.0009) \cdot \text{depth}$

426    $\text{Bout duration}_{\text{FOD 4}} = (8.6 \pm 1.2) + (0.010 \pm 0.0012) \cdot \text{depth}$

4. Discussion

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

430   We deployed on female SES an innovative miniaturised sonar tag that combines active

431   acoustics with high-resolution movement and bioluminescence sensors to describe

432   fine-scale characteristics of prey targeted by seals, i.e. their acoustic size, escape

433   behaviour, bioluminescent behaviour and gregarious behaviour. Sonar tags were

434   deployed simultaneously with CTD tags to record fine-scale in-situ oceanographic data

435   during prey encounters, offering a unique opportunity to study prey characteristics and

436   behaviour simultaneously in relation to oceanographic conditions in a Southern Ocean

437   deep-diving predator. By deploying this tag on a deep-diving predator that forage on

438   mesopelagic prey, the SES, we were able to get some insights into mesopelagic prey

439   distribution and ecology, allowing a significant advance in our understanding of the

440   functioning of the mesopelagic zone.

4.2.   Insights into mesopelagic prey distribution and habitat

442   All prey were encountered in deep open waters outside the Kerguelen plateau, and

443   were not associated with particular topographic features. Most prey encounters

444   occurred in depths ranging from 100 to 800 m, and were characterised by a clear diel

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445 pattern with shallower encounters at night. However, this diel migration behaviour was

446 most noticeable in warmer waters. Female SES are known to target mesopelagic fish

447 such as myctophids (Cherel et al., 2008), whose ecology is consistent with our results

448 (Catul et al., 2011). Prey acoustic size mostly ranged from 3 to 10 cm, which is close

449 to the main size of myctophids inhabiting Kerguelen waters (Duhamel et al., 2000;

450 Hulley and Duhamel, 2011), although it is important to remember that acoustic and

451 actual sizes are not necessarily similar. Indeed, acoustic size is dependent on target

452 orientation (Burwen et al., 2003), which cannot be controlled for here. However, when

453 a prey escapes, it will likely be at some point oriented in the axis of the sonar beam,

454 so measuring the maximum size of the trace of escaping prey should provide a reliable

455 indication of the prey actual size. Therefore, data collected support the hypothesis that

456 most targets insonified by the sonar tag during prey capture events had a body size

457 consistent with myctophids, or more broadly small size mesopelagic fish and squids.

458 Even if data recorded by sonar tags do not allow for identifying species targeted by

459 seals, it provided some precious information about their acoustic size, bioluminescent

460 behaviour, escape behaviour and gregarious behaviour, allowing us to explore

461 differences in prey types according to functional oceanographic domains (FOD) visited

462 by seals. During their foraging trips, seals visited four FOD distributed along an

463 increasing temperature gradient. FOD 1 and 2 were the coldest, with temperature

464 below 2 and 2.5°C respectively. These two FOD might correspond to cold waters south

465 of the Polar Front, characterised by an upper temperature of 2.8°C at 200 m (Park et

466 al., 1993), with FOD 1 likely influenced by the southern boundary of Southern Antarctic

467 Circumpolar Current, defined by a temperature of 1.6°C at 200 m (Park et al., 1993).

468 On the opposite, FOD 3 and 4 were characterised by an upper temperature of 4-5°C

27

469 and 7°C respectively and correspond to warmer water north to the Polar Front, and

470 close to the Subantarctic Front for FOD 4 (Park et al., 1993).

471 Trawling and acoustic surveys around Kerguelen Islands showed contrasted

472 mesopelagic communities between north and south of the Polar Front. *Krefftychthys*

473 *anderssoni* (1-8 cm) and *Electrona antarctica* (3-10 cm) dominate the myctophid

474 community south of the Polar Front, while *Electrona carlsbergi* (4-10 cm),

475 *Gymnoscopelus fraseri* (5-11 cm)*, G. bolini* (15-28 cm) and *G. braueri* (4-14 cm) are

476 more abundant north of the Polar Front (Collins et al., 2008; Duhamel et al., 2000;

477 Hulley and Duhamel, 2011). The Polar Front is a transition zone between cold Antarctic

478 waters and warmer subtropical waters (Gordon, 1971). By acting as a boundary

479 between two different hydrological regions, it constitutes a barrier for many species,

480 resulting in marked differences in marine communities north and south of the Polar

481 Front (Koubbi, 1993). Therefore, we would expect to observe differences in prey

482 behaviour and characteristics between FOD 1-2 (colder waters, south of the Polar

483 Front) and FOD 3-4 (warmer waters, north of the Polar Front).

484 Prey were slightly larger in FOD 3-4 compared to FOD 1-2, however we expected the

485 size difference to be more pronounced. Nevertheless, we noticed differences in prey

486 behaviour depending on the FOD: the proportion of evasive prey was higher in warmer

487 waters, while the proportion of flashing prey was lower. In addition, diel vertical

488 migration patterns were more pronounced in warmer waters, suggesting that prey

489 encountered north and south of the Polar Front are of distinct species, differing in terms

490 of reactivity, bioluminescent behaviour and diel vertical migration behaviour. Acoustic

491 data recorded by bioluminescence-sonar tags therefore provide novel insights on

492 differences on mesopelagic prey behaviour according to oceanographic conditions.

493   Moreover, for each given FOD, we observed strong differences in prey acoustic size

494   and behaviour according to depth: prey encountered deeper were larger than those

495   encountered in sub-surface layers no matter the FOD visited. Therefore, prey size and

496   behaviour seemed to be structured mostly vertically, as observed in previous studies

497   showing that depth is one of the most important factors in the variability of mesopelagic

498   communities (Cook et al., 2013; Kenchington et al., 2020; Sutton et al., 2010). Hulley

499   et al. (2011) reported that within a myctophid species, larger and older individuals are

500   usually encountered deeper than smaller ones. Therefore, vertical size structuration

501   observed in all FOD visited by our tagged seals is consistent with previous findings

502   and is likely to be related with differences in maturity stages between individual prey

503   and not necessarily be due to differences in targeted species.

504   In addition to observing differences in prey size with depth, we also highlighted

505   differences in prey behaviour along the water column. Bioluminescent prey were

506   mostly encountered in sub-surface layers during both day and night, while we expected

507   to observe them in deeper waters (Haddock et al., 2010). Moreover, non-evasive prey

508   were concentrated to shallow waters during both day and night, while evasive prey

509   were also encountered in deeper waters. This pattern was observed in all FOD visited

510   by seals, even if it was more noticeable in colder FOD as few prey were encountered

511   in sub-surface layers in warmer FOD. Although we would have expected that prey

512   encountered in deeper and therefore colder waters were less evasive due to a slower

513   metabolism (Torres and Somero, 1988), we assumed that deep prey, being larger,

514   were more vigilant than smaller/younger individuals encountered in shallower waters

515   due to an increasing predation risk with prey size (Møller and Erritzøe, 2014).

516   To summarise, prey encountered in colder FOD could mostly belong to Antarctic

517   species such as *Electrona antarctica* or *Krefftichthys anderssoni,* with either adults *K.*

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518   *anderssoni* or juveniles *E. antarctica* in sub-surface layers during both day and night,

519   and adult *E. antarctica* exhibiting diel migration being deeper waters during the day,

520   and going back to the sub-surface layers at night (Duhamel et al., 2000). However, the

521   fact that the sub-surface layers seemed dominated by small, non-evasive and

522   bioluminescent prey that did not perform diel vertical migration may suggest that these

523   prey could be other organisms than myctophids such as small bioluminescent

524   gelatinous low energy content organisms or euphausids (Cotté et al., 2022; Trebilco et

525   al., 2019). In warmer FOD, prey encountered could belong to species associated with

526   the subtropical waters such as the genus *Gymnoscopelus,* larger and faster swimming

527   more evasive myctophid species, usually encountered in deeper waters and known to

528   perform diel vertical migration (Duhamel et al., 2000).

529   **4.3.   Where to hunt?**

530   Seals concentrated most of their foraging activity in FOD 1 and 2, i.e. south of the Polar

531   Front. As observed by Field et al. (2004), Guinet et al. (2014) and McMahon et al.

532   (2019), the southern Polar Frontal zone appears to be a preferred area for seals, as

533   they performed shallower dives in that area compared to FOD 3 and 4. The Polar Front

534   is the main foraging area of many species of birds and marine mammals. This area is

535   characterised by intense mesoscale activity, allowing the concentration of organic

536   material and therefore a high biological production. In particular, the southern Polar

537   Frontal zone is known to gather 80% of the myctophid biomass of the Southern Ocean

538   (Lubimova et al., 1987), making this area particularly interesting for SES.

539   Our main hypothesis was that some habitats showed higher prey accessibility and/or

540   prey quality and were therefore preferred by seals. We found that prey encounters

541   were significantly deeper in warmer FOD during both day and night. This result is

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542   consistent with observations by Guinet et al. (2014), Biuw et al. (2007) and McIntyre et

543   al. (2011), showing that bout depth increases with water temperature. Data recorded

544   during trawling and acoustic surveys revealed a deepening of myctophid community

545   when getting closer to subtropical waters (Hulley and Duhamel, 2011), suggesting that

546   prey were less accessible in warmer FOD compared to cold FOD. Moreover, in warmer

547   FOD, prey tended to be slightly more evasive with higher flight initiation distances. A

548   previous study made on the same dataset showed that seals capturing evasive prey

549   were more likely to initiate energy-costing active chase, while non-evasive prey could

550   be passively captured (Chevallay et al., in revision). Indeed, we also observed that

551   bout duration, a proxy for prey capture difficulty (Goulet et al., 2020), was longer in

552   warmer FOD, suggesting that prey captured in warmer waters induced longer handling

553   and/or pursuit times. Goulet et al. (submitted) revealed that evasive prey were

554   associated with a slower improvement in seals' body condition compared to non-

555   evasive prey by relating body condition gain to prey behaviour in SES. To our

556   knowledge, the only studies on the energy content of mesopelagic prey around

557   Kerguelen Islands focus on two or three myctophid species, and have not shown strong

558   differences in energy content between the species studied (Lea et al., 2002; Van de

559   Putte et al., 2006). So there likely is a trade-off between prey size (and energy content)

560   and energy expenditure SES spent to capture them. More species should be studied

561   to make assumptions on the nutritional value of the various prey encountered by

562   elephant seals in the different FOD visited. However, differences in prey behaviour and

563   accessibility between FOD suggest that larger and deeper prey encountered north of

564   the Polar Front might be less accessible and more difficult to capture, increasing

565   locomotion costs, which might make these environments less profitable for elephant

566   seals.

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4.4. Limits of the study

This study highlights the usefulness of the bioluminescence-sonar tag to infer mesopelagic prey distribution and habitat when deployed on deep-diving predators. However, the main limitation of this method is that sampling is biased by the foraging behaviour of the equipped predator. In particular, it might be difficult to disentangled inter-FOD differences with individual preferences, as not all seals visit all FOD. However, when looking for each individual the differences in foraging behaviour between FOD, inter-FOD differences were more pronounced than the inter-individual differences inside each FOD (see Figure 3), suggesting that there are actual structural differences between FOD that are not related to individual preferences. In addition, it is known that seals oversample areas that favour prey aggregation such as frontal systems (Bailleul et al., 2007; Dragon et al., 2010; Siegelman et al., 2019) and do not sample deep waters at night because of the diel migrating pattern of their prey (Slip et al., 1994). However, the small size of the tag makes it possible to deploy on other diving predator species such as fur seals or penguins that also feed on mesopelagic prey but in different vertical/horizontal areas (Bost et al., 2002; Boyd et al., 1991; Charrassin and Bost, 2001) to increase spatio-temporal covering and get a more complete picture of the distribution of mesopelagic prey in the Southern Ocean. Moreover, there is still some uncertainties regarding the nature of targets insonified by the sonar, as acoustic data can be very challenging to interpret. Subsequently, integrating a camera triggered by acoustic detection to the sonar tag could help validating the actual nature of acoustic targets, enabling to be more precise in the description of mesopelagic prey characteristics.

4.5. Conclusion

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591   Using a novel multi-sensor approach deployed on a deep-diving predator, the SES, we

592   were able to explore the functional relationships between oceanographic parameters,

593   distribution and ecology of mesopelagic prey, and foraging behaviour of their

594   predators. We highlighted differences in prey size and behaviour with depth inside

595   each FOD, as well as differences in prey accessibility and behaviour between FOD.

596   Climate change leads to a deep-reaching ocean warming, and this warming is faster

597   in the Southern Ocean compared to the global average (Gille, 2008). Increase in water

598   temperature can considerably alter organism distributions, e.g. studies made on

599   several fish stocks (Nye et al. (2009) on Northeast USA stocks; Dulvy et al. (2008) on

600   North Sea stocks) revealed a deepening of fish stocks with increasing temperature to

601   reach colder waters that are closer to their temperature ranges (Jorda et al., 2020).

602   Therefore, with ocean warming, prey might be increasingly less accessible, forcing

603   seals to dive deeper, which could lead to significant increase in foraging energy costs

604   and exercise strong selective pressure on larger animals, which are found to dive

605   deeper (Piot et al., 2023).

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