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1     **Physical changes recorded by a deep diving seal on the Patagonian**  
2                    **slope drive large ecological changes**  
3

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21  
22                    **Abstract**

23    The Patagonian slope is the region where Subantarctic waters and bathymetry give rise to physical  
24    and ecological processes that support a rich biodiversity and a large-scale industrial fisheries.  
25    Unique among the species that depend on this region is the deep diving southern elephant seal,  
26    *Mirounga leonina*. We report here on changes in the foraging behavior of a female seal explained by  
27    the combined effect of a cold and high salinity water mass and a decrease in surface chlorophyll-a  
28    concentration. Behavioral and oceanographic data from about 5,000 profiles of temperature,  
29    conductivity, pressure, light and prey encounters were collected within an area ranging 59.5-61°W  
30    and 46-47.5°S, at depths of 300-700 m, on the Patagonian slope, during November-December 2018.  
31    A decrease in temperature (0.15°C) and an increase in salinity (0.03) was found below the mixed  
32    layer, during December. Light data revealed a significant increase of **irradiance** in December  
33    (almost reaching the ocean bottom) associated with a decrease of chlorophyll-a in the upper levels.  
34    Concomitantly, the seal had a different diving behavior in December, foraging near the surface at

35 night and close to the bottom during daylight hours. Also, the seal doubled the prey capture  
36 attempts in December compared to November. This study reveals the importance of ocean physical  
37 properties on seal's diving and foraging behavior, and how this changes, although small, can impact  
38 on seals diet and body composition during their post-breeding trips.

39

40 **Keywords : Southwestern Atlantic Ocean, Patagonian Shelf Slope, Elephant Seals, *Mirounga***  
41 ***leonina*, Malvinas Current.**

42

### 43 **Acknowledgments**

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50

### 51 **1. Introduction**

52

53 The Argentine Continental Shelf is located in the Southwestern Atlantic (Figure 1). The shelf is  
54 broad and relatively shallow, with almost 850 km in its wider zone, a surface area of about 1.2  
55 million km<sup>2</sup>, an extension of 2400 km from north to south, and a smooth slope with a variable  
56 maximum depth ranging between 70 and 200 m [Parker et al., 1996; Violante and Cavallotto, 2011;  
57 Violante et al., 2014]. East of the 200 m isobath, the shelf-break is characterized by a steep slope  
58 that goes from 200 to 4000 m depth. In the upper portion of the slope, biological activity is  
59 enhanced due to large chlorophyll-a (chl-a) blooms during the austral spring and summer [Saraceno  
60 et al., 2005; Romero et al., 2006; Garcia et al., 2008, 2011]. The Malvinas Current (MC), which  
61 detaches from the Antarctic Circumpolar Current's northern front, flows northward along the shelf-  
62 break. The MC carries cold and rich nutrient waters that may play a role in the large chl-a  
63 concentrations through interaction with topography and consequent upwelling [Matano and Palma,  
64 2008]. The collision of the MC with the Brazil Current at ~38°S, makes the confluence region one of

65 the most energetic of the world, with eddies and meanders reaching 50°S eastward of the slope  
66 [Piola et al., 1987; Chelton et al., 1990; Saraceno et al., 2009]. Thus, the shelf-break front and the  
67 upper slope encompass a complex region that concentrates a diversity of top predators and other  
68 species, some exploited by industrial fisheries [Martinetto et al., 2020; [Rey and Huettmann, 2020](#)].  
69 The Southern elephant seal, *Mirounga leonina*, that breed and molt along the coast of the Península  
70 Valdés represent one of the main top predators inhabiting these waters. These continuous and deep-  
71 diving seals spend several months at sea foraging, coming back to the location from where they left  
72 to breed or moult [Lewis et al., 2004]. After leaving the shore, post-breeding females cross the  
73 continental shelf in 3-7 days. They forage for approximately two months in deep waters off the  
74 shelf, while adult males usually forage along the outer part of the shelf break [[Campagna et al.,](#)  
75 [1998, 1999](#)]. [Post-breeding females on deep waters show a dive rate of 2.2 dives/hr and a mean dive](#)  
76 [duration of 22.8 minutes, where the mean dive depth range from the ocean surface to the bottom of](#)  
77 [the continental shelf \(~80 m\) and beyond the shelf-break \(~ 600 m\)](#) [[Campagna et al., 1998](#)]. This  
78 continuous and deep diving behavior lead to the idea of using seals as ocean samplers of physical,  
79 biogeochemical and biological parameters by deploying on them small electronic devices  
80 (biologgers) allowing the conduction of a broad range of studies linking seals foraging behavior to  
81 the oceanographic environment [[MEOP project](#); [Boehlert et al., 2001](#); [Guinet et al., 2014](#); [Della](#)  
82 [Penna et al., 2015](#)].

83  
84 Taking advantage of the high frequency temperature, salinity, light, pressure and accelerometry  
85 measurements obtained with the instruments carried by one seal, we investigated how ocean bio-  
86 physical features changed and how its foraging behavior and success responded to those  
87 environmental changes. This paper also aimed at investigating the consistency between satellite  
88 measurements (temperature and chl-a) as well as CMEMS (Copernicus Marine Environment  
89 Monitoring Service) model outputs with the in-situ hydrographic profiles provided by one seal.

90

## 91 **2. Data and Methods**

### 92 **2.1 In situ data**

93

94 As part of an international collaboration between the Centre National de la Recherche Scientifique  
95 (CNRS), the Wildlife Conservation Society (WCS), the University of Tasmania (UTAS) and the  
96 University of Buenos Aires (UBA), nine adult female seals were tracked along the Patagonian shelf  
97 and outer ocean during the austral spring 2018. Following deployment procedures described in  
98 Campagna et al. [1998, 1999, 2006], seals were equipped with positional Argos and/or GPS  
99 systems, as well as different high frequency sampling sensors that record depth (pressure),  
100 temperature, conductivity, fluorescence, irradiance (light), and acceleration (Table 1). In oceanic  
101 Case 1 waters (i.e. waters whose optical properties are determined primarily phytoplankton  
102 concentration and dissolved organic matter), light attenuation (i.e. the variation of the irradiance  
103 signal with depth) quantifies the amount of light arriving at the ocean surface and is independent to  
104 solar angle and cloud cover, thus, it can be used as a proxy of phytoplankton concentration [Bricaud  
105 et al., 1998; Mobley et al., 2004; Jaud et al., 2012; Bayle et al., 2015]. The higher the phytoplankton  
106 concentration the greater is light attenuation from the surface within the water column (Jaud et al.,  
107 2012). Acceleration measurements associated with head movements provide an index of prey  
108 capture attempts (PCA) (see Goulet et al., 2019). Satellite tags and data loggers were deployed in  
109 October 2018, Península Valdés, Argentina, on breeding seal females prior to their departure to the  
110 sea for their post-breeding foraging trip. At the end of their foraging trip, females return to shore.  
111 After being located thanks to the satellite tag, they were recaptured to recover the loggers. For this  
112 study we focus in only one seal (ID 14903) that, after leaving Península Valdés on October 25,  
113 2018, spent two months foraging in a relatively small region over the slope, near the 600 m isobath,  
114 and returned to the same departure location on January 10, 2019 (Figure 1). The studied seal was  
115 equipped with a CTD-SRDLT tag [Boehme et al., 2009], including Argos transmitter (PPT), light  
116 and accelerometry (12.5 Hz) sensors (Table 1). After recovering, the tag was calibrated following

117 the methodology from MEOP described in Roquet et al., [2001] and Siegelman et al., [2019]. The  
118 accuracy of each profile location is of the order of 2 km [Boehme et al., 2009].

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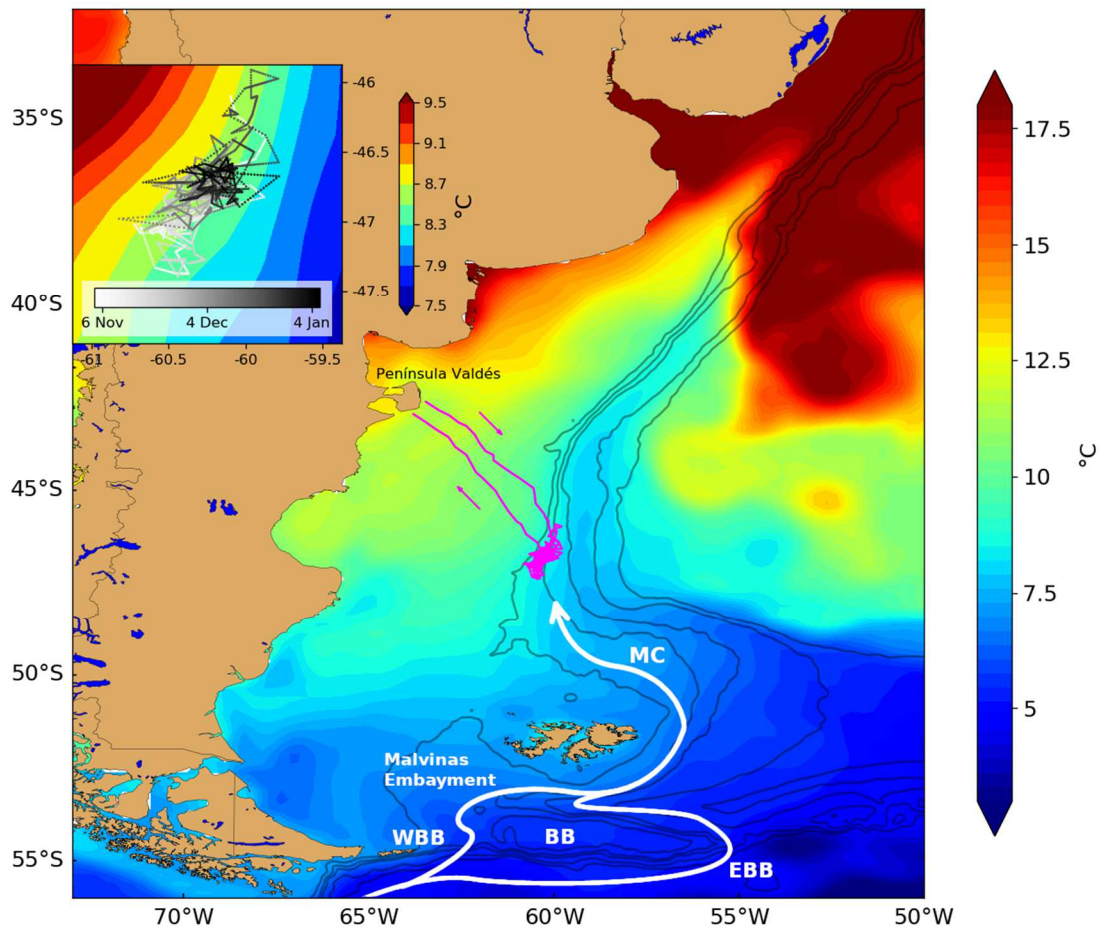
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135 Figure 1. Tracks for the 73-day trip of one seal (magenta line) overlapping monthly-mean sea surface temperature (°C) for November  
136 2018 from OSTIA (see section 2.3). Magenta arrows indicate direction of trajectory. The 200, 600, 1000, 2000 and 3000 m isobaths  
137 are indicated with thin black lines. The white arrow illustrates the main path of the upper slope portion of Malvinas Current (MC)  
138 through the western (WBB) and eastern (EBB) passages of the Burdwood Bank (BB). The top left inset zooms into the trajectory on  
139 the slope. Note that the scale of the temperature contours is different.

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147 Table 1. Main characteristics of the instruments deployed on the studied seal.

CTD-SRDL	Range	Accuracy	Resolution	Frequency
Temperature	-5 to 35 °C	± 0.005°C	0.001°C	2 Hz
Salinity	0 to 50	± 0.01	0.002	2 Hz
Pressure	0 to 2000 dBar	2 dBar ± 0.01% / K	0.05 dBar	2 Hz
Light	$8.31 \times 10^{-7}$ to 3000 $\mu\text{mol}/\text{m}^2\text{s}$	1%	0.1%	2 Hz

148

149

150 For the purpose of this study, and based on the sensor's accuracy, only dives deeper than 15 meters  
 151 were considered. Bottom depth, light and the temperature profiles associated with each dive were  
 152 extracted following the methodology described in Dragon et al., [2012a]. Each dive was divided  
 153 into a descent, bottom and ascent phase. The bottom phase corresponds to the period between the  
 154 end of the descent and the beginning of the ascent. The different dive phases were defined  
 155 according to Dragon et al., [2012a] using a custom-written MATLAB code (version 7.0.1; available  
 156 on request). Accelerometer data was processed following Viviant et al., [2010] and Gallon et al.,  
 157 [2013] using custom-written MATLAB code (available on request) to assess PCA. While PCA  
 158 provide fine scale insights of local variations of prey encounters, seal net foraging gain can be  
 159 assessed by monitoring change in seal body density (i.e. the change in the relative proportion in  
 160 between lipid and protein content) through its foraging trip. This is achieved by monitoring of the  
 161 descent rate, when the seal is sinking passively through the water column during special  
 162 resting/food processing dives qualified as 'drift dives' [Crocker et al., 1997; Biuw et al., 2003]. The  
 163 descent speed during these drift phases is directly related to buoyancy, with more buoyant seals (i.e.  
 164 with a higher lipid proportion) sinking at a slower rate compared with leaner ones [Crocker et al.,  
 165 1997; Biuw et al., 2003; Miller et al., 2012]. However, such 'drift rate' data obtained from time-  
 166 depth recorder tags can only provide a general temporal trend in body composition change and with  
 167 a temporal lag of about 3 to 6 days compared to change of PCA rate [Dragon et al., 2012b; Richard

168 et al., 2014, 2016]. Each dive was attributed to either day or night periods. This was defined  
169 according to the solar angle, taking into account the geographical location of the seal provided by  
170 the Argos transmitter and the time at the beginning of the dive (see Guinet et al., 2014).

171  
172 The animal spent most of the time in a boundary region with strong year-round zonal temperature  
173 gradients (Figure 1, inset-panel), generated by the cold MC waters and the warmer continental shelf  
174 waters [Saraceno et al., 2004; Piola et al., 2013]. Over the two-month period, the seal tended to dive  
175 mostly in the southwestern part of the foraging area in November and in the northeastern part in  
176 December (Figure 1, inset-panel). Thus, to be able to compare the monthly mean temperature and  
177 salinity between November and December, the zonal movement of the seal was taken into account.  
178 To achieve this, we kept only with a sub-sample of the data (~28% of the total dives in the upper  
179 slope, i.e. 1146 from 4150 total profiles) after dividing the area in equal longitudinal bins and  
180 selecting the same amount of profiles on each longitude bin for November and December,  
181 discarding the rest. The selection of the discarded profiles was done randomly. This methodology  
182 was repeated a hundred times, to compute finally a mean temperature averaged from the hundred  
183 samples.

## 184 185 **2.2 Numerical model and reanalysis data**

186  
187 The Operational Mercator global ocean analysis and forecast system (PSY4QV3R1) is based on  
188 NEMO ocean model [Madec et al., 2019] and provides 3D global ocean forecasts updated daily,  
189 starting in January 2016 for daily outputs and January 2007 for monthly outputs. It has a 1/12°  
190 degree horizontal resolution with regular longitude/latitude equi-rectangular projection, resolved  
191 over 50 vertical levels, ranging from 0 to 5500 m. Model outputs include daily and monthly mean  
192 files of temperature, salinity, currents, sea level and mixed layer depth among others. Comparison  
193 with satellite and Argo float data showed that the system correctly reproduced the general  
194 circulation and the complex hydrographic features of the Southwestern Atlantic Ocean (Artana et



195 al., 2018b). Model data is available through Copernicus Marine Environment Monitoring Service  
196 (CMEMS, <http://marine.copernicus.eu/>). To compare seal data with model, we downloaded daily  
197 values of temperature and salinity for the levels corresponding to the 0-600 m depth range in seal's  
198 foraging domain (46.2-47.3°S and 60.7-59.8°W). Valid seal measurements (after sensors stabilize in  
199 the water column) begin at ~18 m depth, thus, model values from 18 m were interpolated to seal  
200 location. Finally, a 4-hour moving average was applied to both series. For the temperature-salinity  
201 diagram (Figure 4), seal profiles were selected when the distance between a given profile and the  
202 nearest model grid point was less than 1 km. This procedure provided a total of 205 profiles for  
203 each data set. Also, to have the same number of vertical values per profile, we selected the values  
204 from the seal records that coincide with a depth level of the model (i.e. 32 levels, from the surface  
205 to 550 m).

206 Cloud cover mentioned in Section 3.2 is a product of ERA5 global reanalysis. We used monthly  
207 values of cloud area fraction in seal's foraging region, with a spatial resolution of 0.25°. Data is  
208 available at <https://cds.climate.copernicus.eu/cdsapp#!/home>

209

## 210 **2.3 Satellite data**

211

212 Sea surface temperature (SST) considered here was produced by the Group for High Resolution  
213 Sea Surface Temperature (GHRSSST) and is provided by the Operational Sea Surface Temperature  
214 and Ice Analysis (OSTIA). The product merges in situ data, infra-red and micro-wave radiometers  
215 and has a 0.05° x 0.05° horizontal resolution [Bell et al., 2000; Stark et al., 2007; Donlon et al.,  
216 2012]. Near real time L4 product was downloaded from <http://marine.copernicus.eu/>. To compare  
217 SST with seal temperature measurements at 18 m (Figure 3a), data was interpolated to seal location  
218 and finally a 4-hour moving average applied.

219

220 Monthly mean composites and daily gridded L3 chlorophyll-a concentration MODIS-Aqua ocean  
221 color data, with a spatial resolution of 4 km from the Ocean Biology Processing Group  
222 (NASA/GSFC/OBPG) were downloaded from <https://oceandata.sci.gsfc.nasa.gov>.

223

### 224 **3. Results**

225

226 Sixty-three days out of the 73 day-long foraging trip were spent on the slope of the Patagonian  
227 shelf break (Figure 1). The seal covered 4,500 kilometers and performed a total of 4,951 dives (i.e.  
228 hydrographic profiles), from which 92% of them occurred over the slope. In this study we focus  
229 only on the data provided by the seal while foraging over the Patagonian slope from 4 of November  
230 2018 to 6 of January 2019.

231

#### 232 **3.1 Physical environmental changes**

233

234 Temperature and salinity profiles evidenced contrasted oceanographic changes over the study  
235 period between a warming upper layer (0-35 m) and cooling waters below (from 50 m to the  
236 bottom; Figure 2). In the upper layer, the depth-averaged temperature increased (1.6°C) within the  
237 two months due to higher net incoming heat radiation associated with the arrival of austral summer  
238 (Figure 2a). This change in temperature was accompanied by a salinity increase of 0.09 in the upper  
239 35 m, enhanced in the last two weeks (Figure 2b). Waters below the upper layer show a very  
240 different behavior, with a mean temperature decrease in December of 0.25°C (Figure 2a) and an  
241 increase in salinity of 0.04 (Figure 2b). If we minimize the zonal displacement of the seal (see  
242 methods, Section 2.1), the temperature decrease and salinity increase in the subsurface layer  
243 accounts for 0.15°C and 0.03 respectively.

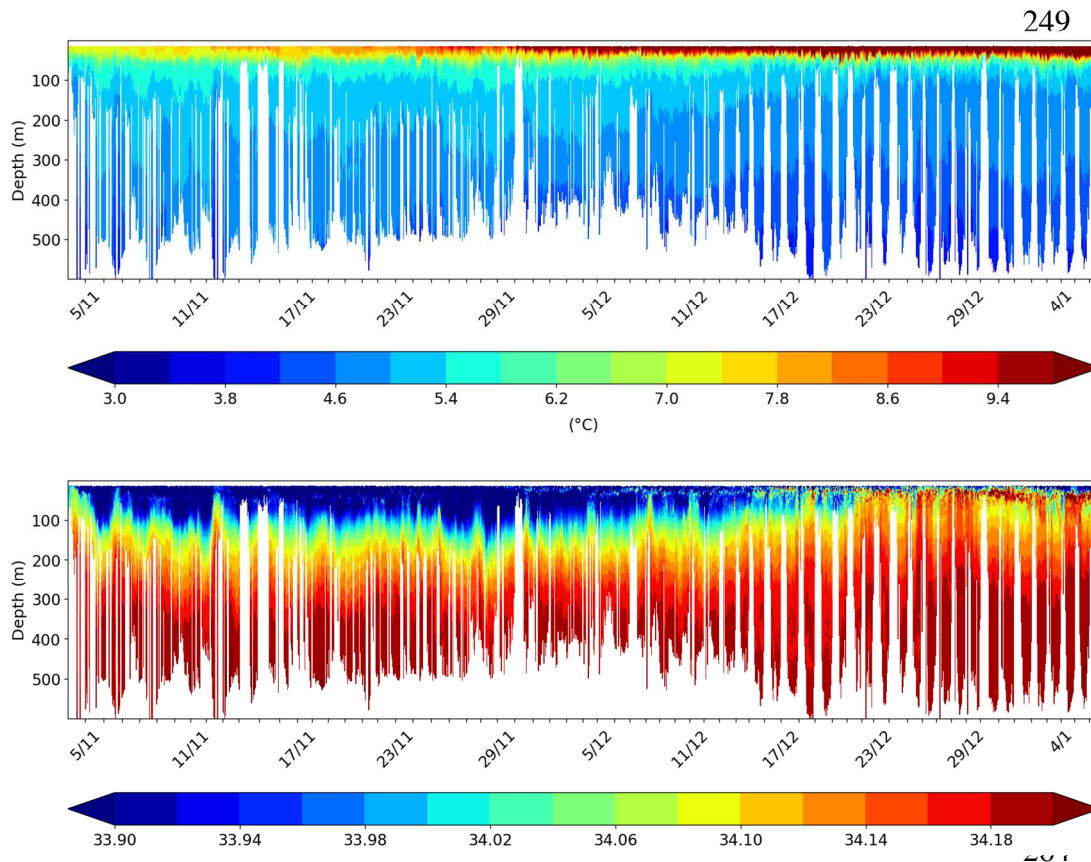
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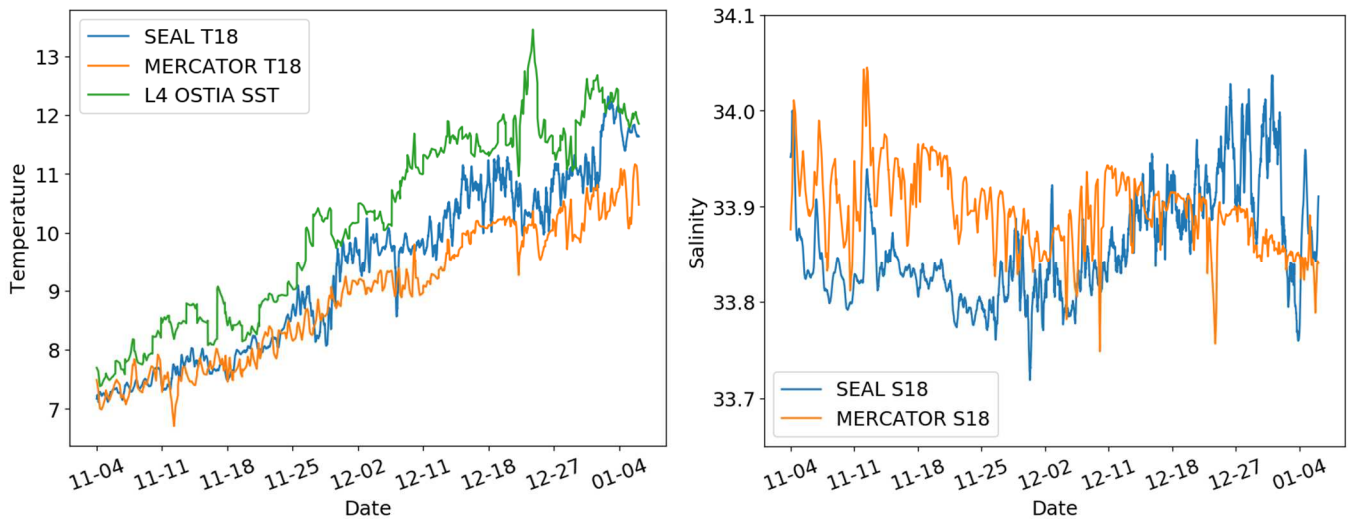


265 Figure 2. Temperature (°C, upper panel), and salinity (bottom panel) profiles measured by the seal in the Patagonian slope (top and  
266 bottom panels respectively).

267

268 Near surface temperature (T18) and salinity (S18) values obtained by the seal were compared with  
269 those from Mercator model and satellite observations following procedures described in Section 2  
270 (Figure 3). The seal T18 signal presented visible discrepancies compared to Mercator temperature at  
271 18 m and to OSTIA L4 surface values. Temperatures recorded by the seal were lower than OSTIA  
272 during both months, and slightly higher than Mercator in December. Also, there were amplitude  
273 differences between seal data and both series that result in a root mean square error of  $0.62^{\circ}\text{C}$  with  
274 OSTIA and  $1^{\circ}\text{C}$  with Mercator. Nevertheless, they all described the same temperature increase  
275 pattern during both months, and were highly correlated ( $r = 0.91$  with Mercator and  $r = 0.94$  with  
276 OSTIA, at the 99% significance level) (Figure 3, left panel). As we were unable to compare our data

277 with satellite surface salinity measurements with spatial and temporal resolution comparable to the  
 278 horizontal diving range of the seal, we only compared salinity recorded by the seal and Mercator  
 279 outputs at 18 m (Figure 3, right panel). Mercator salinity showed higher values in November and  
 280 early December compared to our data (root mean square error = 0.08), and a salinity decrease since  
 281 December 11, the opposite of what was observed in our records, that increased during all December.  
 282 Also, the two-month salinity time series were not significantly correlated; yet, if we split the series  
 283 by month we found a significant correlation in November ( $r = 0.5$ ), and no correlation in  
 284 December.



285

286 Figure 3. Four hours moving average of temperature at 18 m from seal records (blue) and Mercator (orange) and at surface for  
 287 OSTIA (green) (°C, left panel). Right panel shows the salinity from seal records at 18 m (blue), Mercator (orange).

288

289 Subsurface data obtained by the seal in the upper slope were compared with those from Mercator  
 290 model in a temperature-salinity diagram (Figure 4) following the methodology explained in Section  
 291 2.2. Following the water masses definitions described by Piola and Gordon [1989] and by  
 292 Maamaatuaiahutapu et al. [1994], the temperature and salinity distribution indicated that the  
 293 foraging region of the seal was composed mostly of three water masses: Subantarctic Surface  
 294 Waters (temperature  $> 5^{\circ}\text{C}$ , salinity  $\sim 33.82$ ), Subantarctic Mode Waters (temperature  $\sim 4.7^{\circ}\text{C}$ ,  
 295 salinity  $\sim 34.19$ ) and Upper Antarctic Intermediate Waters (temperature  $< 4^{\circ}\text{C}$ , salinity  $\sim 34.18$ )

296 (Figure 4a). A closer inspection of the bottom water distribution (blue box in Figure 4a) is coherent  
297 with the  $\sim 0.15^{\circ}\text{C}$  December cooling observed in Figure 2, while a salinity change was  
298 imperceptible (Figure 4b). Some major differences arise when comparing seal data with Mercator  
299 temperature-salinity distribution. Subantarctic Surface Water for model distribution were less  
300 disperse in salinity but showed a strong dispersion in the transition through Subantarctic Mode  
301 Waters, that, in turn, presented a higher temperature, reaching  $6^{\circ}\text{C}$  (Figure 4c). The Antarctic  
302 Intermediate Waters for model data (blue box in Figure 4c) appeared as two distinct waters masses,  
303 one fresher and other saltier and slightly colder, the former being from November and the latter  
304 from December (Figure 4d). The cooling observed in December may be due to intrusions of the MC  
305 core [Piola et al., 2010; Matano et al., 2010; Combes and Matano, 2014] or to the increased  
306 transport of Upper Antarctic Intermediate Waters from the Eastern passage of the Burdwood Bank  
307 [Piola and Gordon, 1989; Matano et al., 2019].

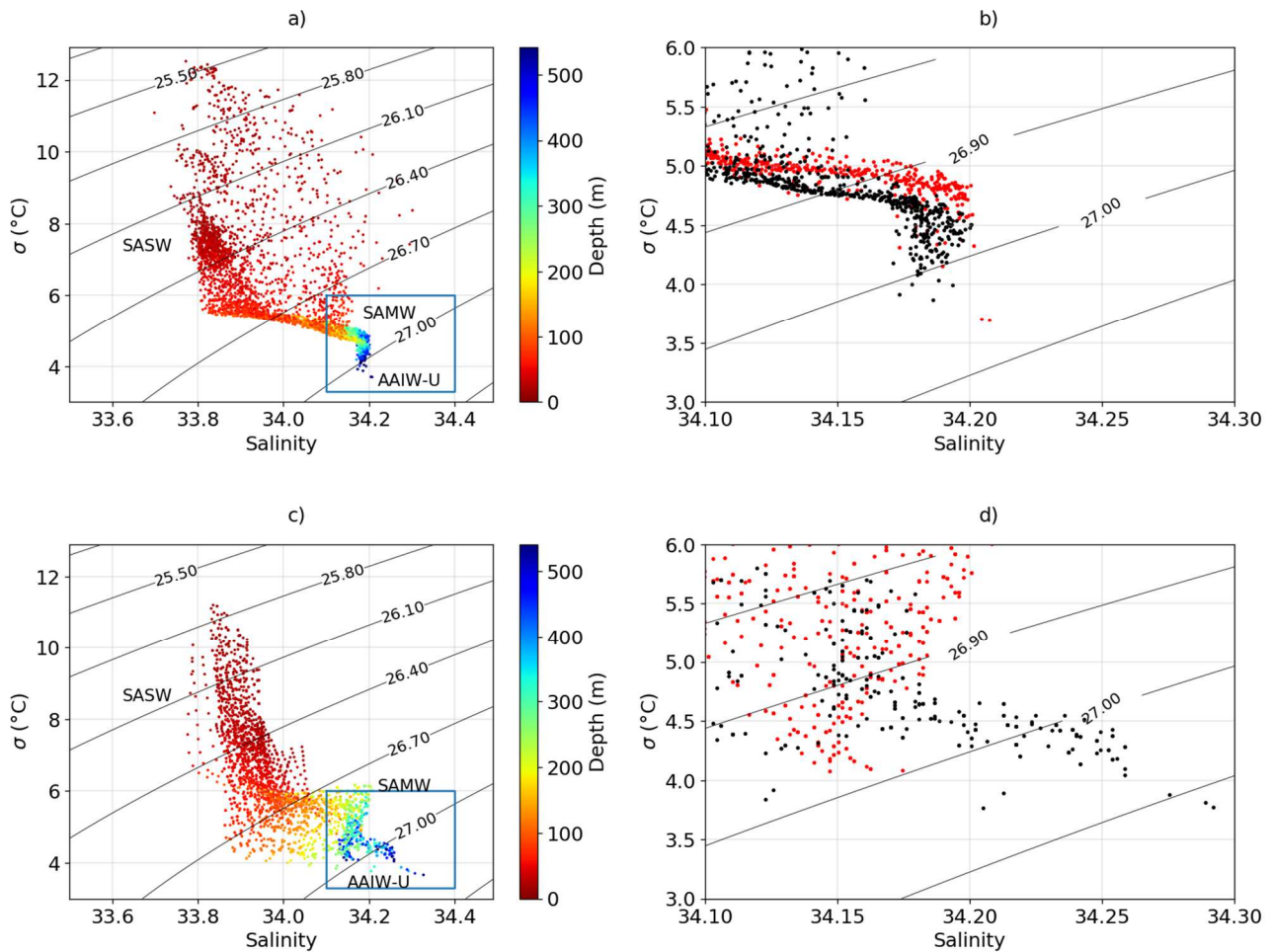
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 314 Figure 4. Potential temperature – salinity diagrams from data recorded by the seal (a) and Mercator outputs (c). The colorbar  
 315 indicates the depth of each dot and the gray lines the potential density isolines (sigma-theta). Deep waters (indicated with a blue box  
 316 on both diagrams) are amplified in panel b) for the data recorded by the seal and panel d) for Mercator. The red dots in panels b and d  
 317 correspond to November data and the black ones to December. The different water masses are indicated in panels a,c as SASW  
 318 (Subantarctic Surface Waters), SAMW (Subantarctic Mode Waters) and AAIW-U (Upper Antarctic Intermediate Waters).

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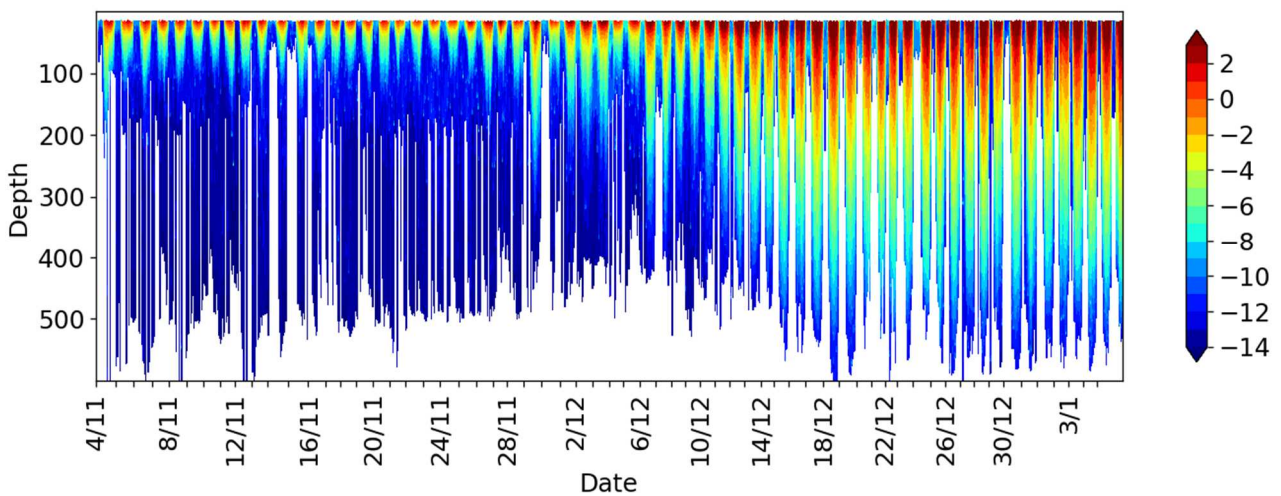
### 320 3.2 Change in phytoplankton concentration

321

322 Light attenuation in open ocean waters partially depends on the concentration of inorganic and  
 323 organic particles suspended within the water column. In particular, phytoplankton (quantified  
 324 through active measurement of chlorophyll-a fluorescence) constitutes the main source of particles  
 325 in suspension within the euphotic layer, and it has been shown to be the main cause of light  
 326 attenuation for Case 1 waters [Bricaud et al., 1998; Jaud et al., 2012]. In November, the irradiance  
 327 in the Patagonian upper slope region, where the seal spent time, reached more than -8 ln

328 ( $\mu\text{mol}/\text{m}^2/\text{s}$ ) only in the upper 150 m of the water column (Figure 5). However, the same amount of  
329 irradiance reached 500 m depth in December, revealing a sharp decline in phytoplankton  
330 concentration. Seasonal solar incidence angle and daylight duration also contributed, in a minor  
331 way, to light increase in December. Cloudiness also affects the amount of light that reaches the  
332 ocean surface. However, total cloud cover was higher in December compared to November (not  
333 shown). Thus, the irradiance increase observed between November and December can be mostly  
334 explained by the decrease in chlorophyll-a (chl-a hereafter) concentration.

335



336 Figure 5. Amount of light (irradiance) as logarithmic photosynthetic photon flux density ( $\ln(\mu\text{mol}/\text{m}^2/\text{s})$ ) along depth (m) measured  
337 by the seal in the slope region during November and December.

338

339 In-situ assessments of phytoplankton concentration were consistent with the MODIS-Aqua ocean  
340 color satellite measurements over the study period for November 2018 (Figure 6a). This result  
341 revealed large amounts of chl-a ( $> 6 \text{ mg}/\text{m}^3$ ) over the region where the seal dove, and over the 200  
342 m isobath, the shelf-break front (SBF). These large concentrations of chl-a generated a barrier of  
343 suspended particles that inhibited light beyond the upper layers. In December 2018 (Figure 6b), the  
344 chl-a concentration decreases ( $< 2 \text{ mg}/\text{m}^3$ ), thus allowing the light to reach greater depths. The chl-a  
345 concentration decrease was also observed in daily MODIS-Aqua ocean color chl-a and surface chl-a  
346 concentration estimated by seal irradiance data and a linear functional model (LFM) (Figure 6c).

347 The linear functional model described in Bayle et al. 2015 is a predictive tool enabling to infer chl-a  
348 concentration from irradiance along the water column through a per-profile functional approach  
349 based on a learning dataset of concomitant vertical profiles. Light in the ocean has a direct  
350 correlation with the vertical distribution of many marine organisms, ranging from zooplankton [Liu  
351 et al., 2003] to fish [Batty et al., 1990] and marine mammals [Horning and Trillmich, 1999].  
352 Elephant seals depend on suitable and abundant prey (fishes and squid) present at the fronts  
353 [Campagna et al., 2007; Eder et al., 2010]. The area frequented by the studied animal, is associated  
354 with the SBF. The SBF has high concentrations of chl-a and high primary production, which would  
355 attract organisms of different trophic levels [Martinetto et al., 2020]. Moreover, the SBF is an area  
356 of intense fishing activity [Portela et al., 2012; Alemany et al., 2014] (Figure 6a,b). The main  
357 commercial species, at different times of the year, are Patagonian grenadier (*Macruronus*  
358 *magellanicus*), shortfin squid (*Illex argentinus*) and Argentine hake (*Merluccius hubbsi*) [Portela et  
359 al., 2012; Alemany et al., 2014]. Figure 6a,b shows that the fishing effort (in hours, Global Fishing  
360 Watch, 2020) in the SBF was much larger in December 2018 (18031 hours) than in November 2018  
361 (4841 hours), and that the international fishing fleet concentrated north of the seal foraging ground.  
362 Figure 6 also shows that the largest fishing activity along the shelf-break did not correspond to the  
363 period of time when the largest chl-a concentration was observed.

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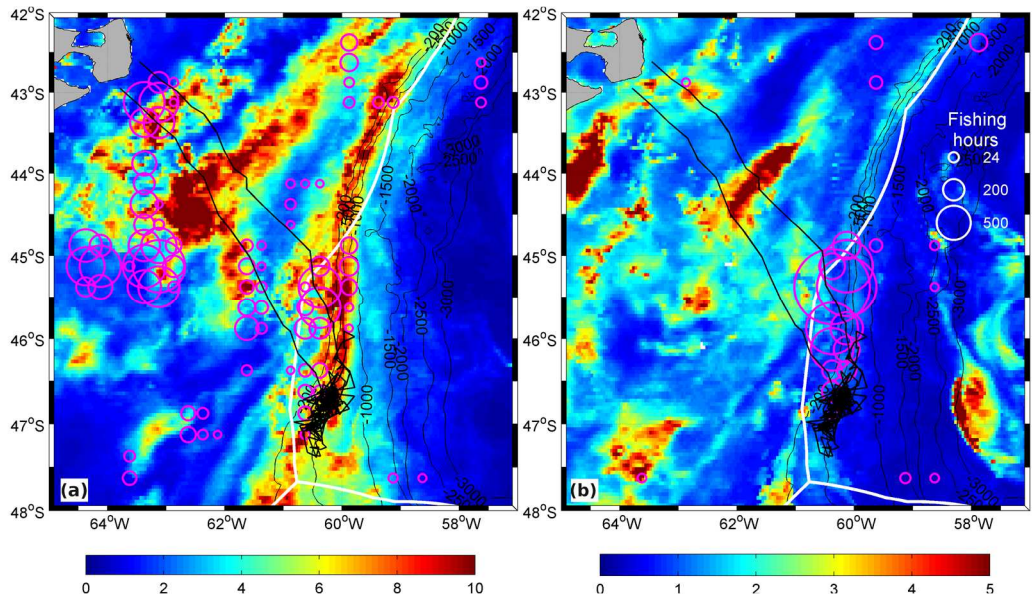
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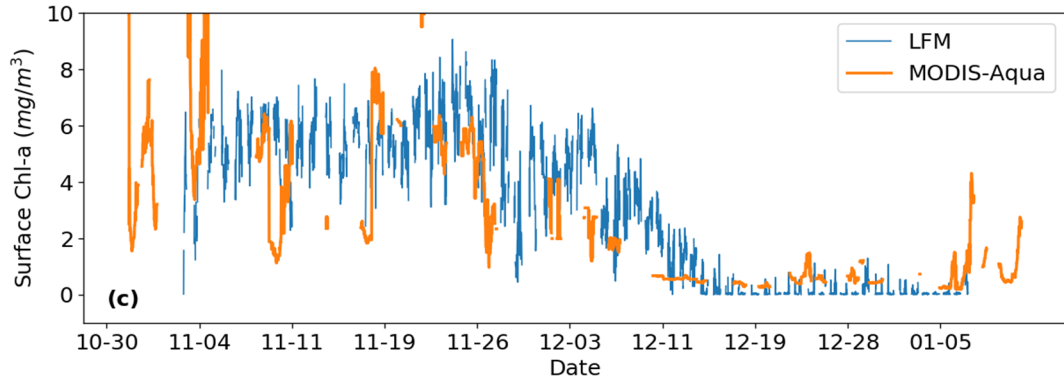
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Figure 6. Modis-Aqua monthly mean chl-a concentration ( $\text{mg}/\text{m}^3$ ) for November (a) and December (b) 2018. The magenta circles represent the fisheries activity for each month, the size is proportional to the fishing effort (hours). The white line represents the limit of the Argentine Exclusive Economic Zone. The black lines indicate the seal trajectory and the isobaths. Daily surface chl-a concentration (c) in  $\text{mg}/\text{m}^3$  for satellite Modis-Aqua (orange) and estimated by the LFM method (blue).

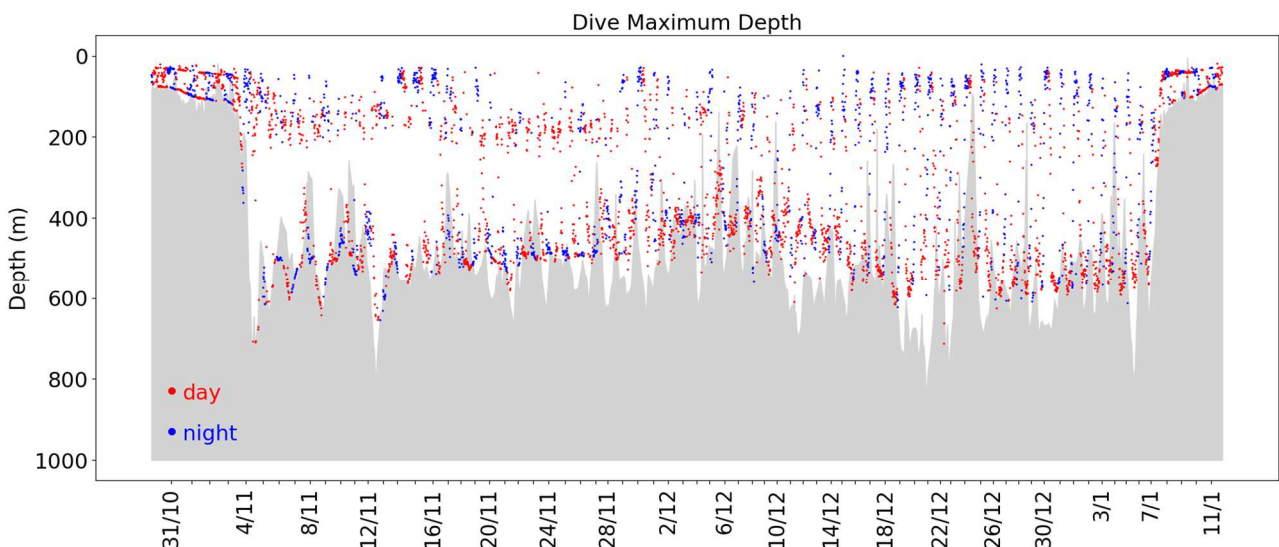
### 3.3 Elephant seal foraging behavior

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406 The overall mean diving depth of the seal was  $263.8 \pm 192.0$  m at night, with a mean dive duration  
407 of  $17.4 \pm 4.3$  minutes. During the day, the mean diving depth was  $331.5 \pm 186.7$  m, with a mean  
408 dive duration of  $19.8 \pm 3.9$  minutes.

409 To better understand how ocean dynamics and light can affect elephant sea foraging behavior we  
410 analyzed dive maximum depth (DMD) for each dive, and number of PCA performed. In November,  
411 DMD were either on shallow waters (<200 m) or sweeping the ocean bottom, avoiding the middle  
412 depths and with a minor difference between day and night (Figure 7). The sea floor (shading gray in  
413 figures 7 and 8) is an interpolation of GEBCO 2019 bathymetry (15 arc-second resolution) to seal  
414 diving locations, and DMD extending beyond the sea floor are due to possible errors on seal  
415 location or bathymetric chart product. In December, the animal dove predominantly (58%) near the  
416 surface at night (blue dots in Figure 7), and reached the ocean bottom (80%) during the day (red  
417 dots in Figure 7). The mean DMD increased from  $337.5 \pm 173.7$  m in November to  $359.4 \pm 180.4$  m  
418 in December and the mean dive duration increased from  $17.6 \pm 3.5$  minutes in November ( $9.4 \pm 3.3$   
419 minutes in the bottom phase) to  $19.6 \pm 4.5$  minutes in December ( $11.1 \pm 4.0$  minutes in the bottom  
420 phase).

421



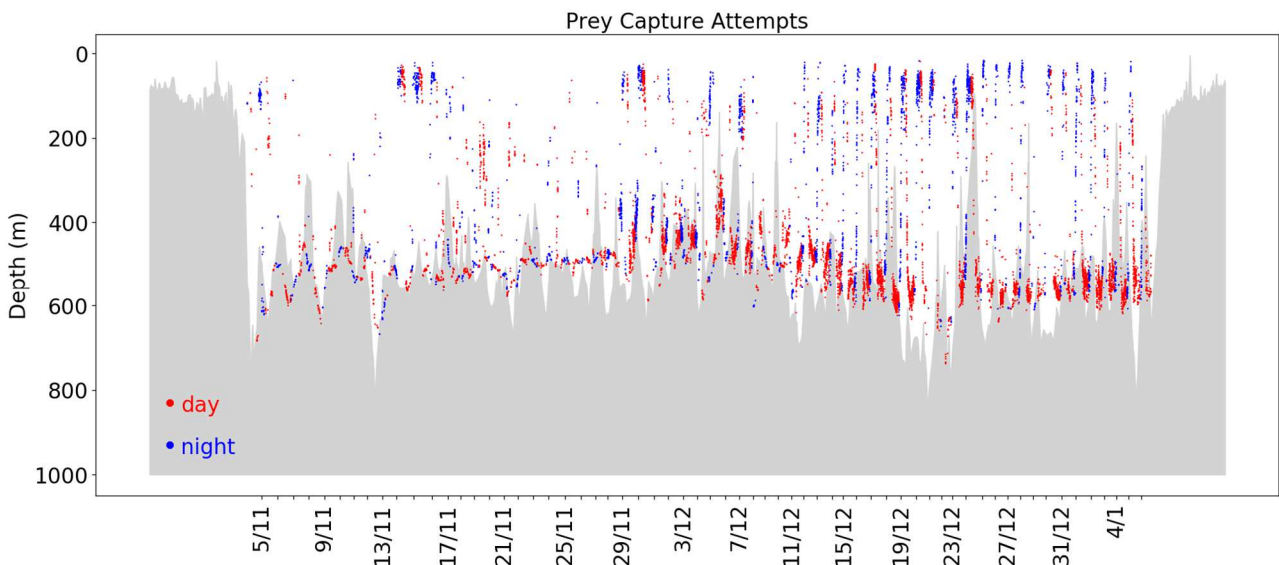
422 Figure 7. Dive maximum depth (DMD) with different colors for day (red) and night (blue). The shading gray is the bottom

423 topography from GEBCO 2019 interpolated along the elephant seal diving trip.

424

425 Compared to November, December was characterized by a significant increase in number of PCA  
426 (287 versus 125 PCA per day) (Figure 8). Statistics for both DMD and PCA are summarized in  
427 Table 2. In agreement with early studies [Guinet et al., 2014; Gallon et al., 2013; Schreer et al.,  
428 2001], the majority of the PCA (~86%) occurred during the bottom phase of the dive. In November,  
429 77% of the observed PCA were skimming the ocean bottom, both during day (red dots) and night  
430 (blue dots) and with the particularity that an increase of PCA near the surface can be seen between  
431 13-17 of November (Figure 8). In December, the majority of the PCA occurs in the upper (< 300 m)  
432 part of the water column during night (54%) and in the lower part (> 300 m) during daylight hours  
433 (89%). A strong decrease of PCA, especially near the ocean bottom was observed between 21-23 of  
434 December.

435



436 Figure 8. Depth location of prey capture attempts (PCA) with different colors for day (red) and night (blue). The shading gray is the  
437 bottom topography from GEBCO 2019 interpolated along the elephant seal diving trip.

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448 Table 2. Total dives and percentages of DMD and PCA during November and December 2018. Upper water column (< 300 m) and  
 449 lower water column (> 300 m).

	Dives		DMD		PCA	PCA	
	Total	Mean Duration (minutes)	Upper Water Column (%)	Lower Water Column (%)	Total	Upper Water Column (%)	Lower Water Column (%)
<u>November</u>	2093	17.6	40	60	3745	23	77
Day	1285	18.5	41	59	2194	20	80
Night	808	16.8	38	62	1551	29	71
<u>December</u>	2050	19.6	34	66	8617	24	76
Day	1287	21.2	20	80	5967	11	89
Night	763	18.0	58	42	2650	54	46

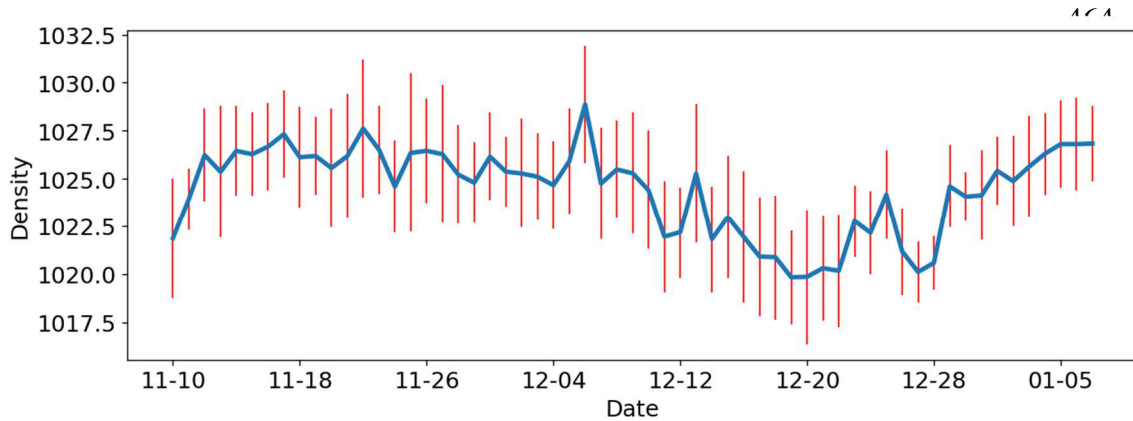
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452 The monitoring of the female body density, reveals that seal density increased to remain high  
 453 through the whole month of November and started to decrease (i.e. improvement of body condition  
 454 due to an increase in lipid content, which is linked to a higher prey ingestion) by early December  
 455 (Figure 9), which matches well with the change in environmental conditions (keeping in mind that  
 456 there is a lag of 3 to 7 days between prey ingestion and body density changes [Dragon et al., 2012b;  
 457 Richard et al., 2014, 2016]).

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472 Figure 9. Seal daily mean density ( $\text{kg/m}^3$ ) estimated along the trip (blue line) and standard deviations (red lines).

473

#### 474 **4. Summary and Discussion**

475

476 High frequency data collected along the upper portion of the Patagonian slope during November  
477 and December 2018 by one post-breeding female elephant seal equipped with multiple sensors was  
478 used to investigate the interaction between ocean dynamics and seal diving and foraging behavior.  
479 Measurements obtained by the seal showed a decrease in temperature ( $0.15^\circ\text{C}$ ) and a salinity  
480 increase (0.03) below the mixed layer during December in the Patagonian slope, at  $46\text{-}47.5^\circ\text{S}$ .  
481 Temperature outputs from Mercator model at 18 m and OSTIA satellite data were in agreement with  
482 the increase pattern observed from seal data at 18 m. Nevertheless, our records showed higher  
483 temperatures than Mercator in December, and discrepancies in amplitude oscillations. On the other  
484 hand, salinity outputs from Mercator showed major differences with that obtained by the seal at 18  
485 m, mostly in December, when Mercator data showed an opposite pattern. The differences between  
486 seal and Mercator data may be due to a mismatch between seal location and ARGOS positioning  
487 system, but also to the fact that seal's data used for the comparison was from around 18 meters

488 (where sensors stabilize and give more accurate measurements). Given that temperature and salinity  
489 profiles recorded by the seal indicate a mixed layer depth of ~25 m in November and ~18 m in  
490 December (not shown), measuring at this depth level may lead to uncertainties, mostly in  
491 December. Also, SRLD-CTD sensors could suffer an erosion of its accuracy during the seal's trip,  
492 specially for salinity measurements [Santini et al., 2018]. Light data also revealed a significant  
493 increase of irradiance in December (almost reaching the ocean bottom) associated with a decrease  
494 of chl-a in the upper levels revealed by our records and satellite Modis-Aqua data. Indeed, the  
495 largest concentration of chl-a values in the Patagonian shelf and slope are usually observed in  
496 November, during the austral spring bloom [Saraceno et al., 2005; Romero et al., 2006; Rivas et al.,  
497 2006] and start decreasing in December due to nutrient consumption and ocean stratification that  
498 inhibits the upwelling of nutrients to the euphotic zone.

499  
500 Fishing effort in December (larger compared to November,) was concentrated north of the seal  
501 foraging ground. The spatial mismatch between the fishing activity and the seal foraging ground  
502 can be due to several causes, as seal trying to avoid fishing lines and nets and/or a different spatial  
503 distribution or differences in the targeted fish/squids species by seal and fisheries. Indeed, the seal  
504 might be eating preys that are not of commercial interest, like lantern fish (Myctophids) that are  
505 very common in this area [Figueroa et al., 1998; Eder et al., 2010; McGovern et al., 2019]. Yet, we  
506 do not have data to explain the spatial distribution mismatch. Also, the largest fishing activity along  
507 the shelf-break did not corresponded to the period of time when the largest chl-a concentration was  
508 observed. This fact can be explained considering different possibilities: (i) the most interesting  
509 commercial species arrived in December with the colder and saltier water mass observed above; (ii)  
510 the species that took advantage of the large phytoplankton bloom in November grow enough so in  
511 December became prey of commercial species. Last but not least, the fact that both in November  
512 and in December relatively large chl-a concentrations were observed along the upper portion of the

513 Patagonian slope in comparison to adjacent waters is a clear indication that a physical forcing  
514 related to the bathymetry drives the large concentration of chl-a observed.

515

516 The elephant seal also showed a distinct behavior during the two-months trip. In December, the  
517 PCA increased more than double with respect to November with the seal diving preferentially at  
518 surface during the night and in the bottom layers during the day. The increase in PCA observed in  
519 December can be attributed to a higher concentration of prey items due to the arrival of preys with  
520 cold nutrient rich Antarctic Intermediate Waters. This result was also reflected in the larger fishing  
521 effort detected in December. The density change of the seal along the trip, reflected quite well the  
522 increment of PCA at the beginning of December. Moreover, the density increase observed around  
523 the 23-26 of December matched with the observed decrease in PCA between 21-23 of December.  
524 The increase of PCA in December can be seen both in the surface and bottom layers, suggesting that  
525 the arrival preys migrated along the whole water column in response of light variability. Results  
526 also showed that in December DMD increased 6% compared to November (66% of the dives in  
527 December were below 300 m depth against 60% in November) and an increase of 2 minutes in  
528 dives duration. These results are in agreement with previous studies that found a negative  
529 correlation between surface chl-a concentration and both DMD and dive duration [Dragon et al.,  
530 2010].

531

532 The relationship between prey location in the water column and light is known to dominate seals  
533 diving behavior [Jaud et al., 2012; Guinet et al., 2014]. Several studies have shown that light level  
534 precisely controls the vertical distribution of many species, in particular myctophids, which are part  
535 of the seals diet [Catul et al., 2011]. Lower surface chl-a concentration means higher light  
536 penetration, thus a deeper distribution of myctophids species. According to this, seal behavior in  
537 December suggests that shallower dives during the night are related to preys that tend to concentrate  
538 near the surface. During the day, as light increases in the water column, prey items tend to displace

539 to higher depths, and so does the seal, with predominant DMD and PCA near the seabed in  
540 December.

541  
542 We can expect that low [irradiance \(light\)](#) in November due to high chl-a concentration should be  
543 associated with myctophids prey located in shallower waters, conditioning the seal to dive and  
544 forage closer to the surface. However, November data showed that the seal dived predominantly  
545 near the seabed, where most of the PCA were detected. This result suggests that a different prey  
546 item, other than myctophids, can be the main diet for seals in the ocean bottom. This hypothesis is  
547 in agreement with McIntyre et al., [2011] which came to the conclusion that seals can have different  
548 forage strategies and dives, reaching greater depths at night compared with the day and that the  
549 change can be associated with foraging of different prey resources. Furthermore, Goulet et al.,  
550 [2020] suggest that female seals in Península Valdés are mainly pursuing larger or harder to catch  
551 prey that do not produce bioluminescence as a predator defense and are probably more dispersed in  
552 the water column.

553  
554 The Patagonian slope is a very complex region, where subantarctic waters and bathymetry give  
555 raise to a unique area of ecological processes and one of the greatest fisheries in the world. The  
556 uniqueness of simultaneous high resolution in-situ data (physical, biogeochemical and biological)  
557 collected by seals are a valuable resource to address oceanographic research and to calibrate and  
558 validate ocean numerical models and satellite data. In particular, the data obtained from one seal  
559 allowed us to improve our knowledge of the MC in the upper portion of the Patagonian slope, at  
560 47°S, and also to link the sharp change in the water masses to the animal behavior. To deepen this  
561 study, future campaigns in the region are thought to track fully equipped male elephant seals that  
562 are known to dive preferentially in the Patagonian slope. Also, it is planned to incorporate  
563 photographic cameras to the seals to try to unveil the prey items. Complementary data from  
564 fisheries will also help elucidate the diving behavior and forage strategies in the region.



565

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