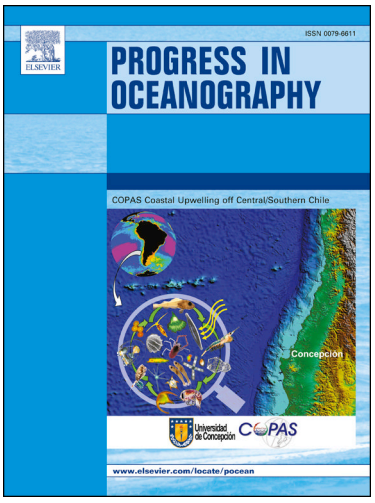
Accepted Manuscript



Under the sea ice: Exploring the relationship between sea ice and the foraging behaviour of southern elephant seals in East Antarctica

Sara Labrousse, Jean-Baptiste Sallée, Alexander D. Fraser, Robert A. Massom, Phillip Reid, Michael Sumner, Christophe Guinet, Robert Harcourt, Clive McMahon, Frédéric Bailleul, Mark A. Hindell, Jean-Benoit Charrassin

PII: S0079-6611(16)30044-1
DOI: http://dx.doi.org/10.1016/j.pocean.2017.05.014
Reference: PROOCE 1812

To appear in: *Progress in Oceanography*

Received Date: 9 March 2016
Revised Date: 7 April 2017

Please cite this article as: Labrousse, S., Sallée, J-B., Fraser, A.D., Massom, R.A., Reid, P., Sumner, M., Guinet, C., Harcourt, R., McMahon, C., Bailleul, F., Hindell, M.A., Charrassin, J-B., Under the sea ice: Exploring the relationship between sea ice and the foraging behaviour of southern elephant seals in East Antarctica, *Progress in Oceanography* (2017), doi: http://dx.doi.org/10.1016/j.pocean.2017.05.014

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

ACCEPTED MANUSCRIPT

Under the sea ice: Exploring the relationship between sea ice and the foraging behaviour of southern elephant seals in East Antarctica.

Labrousse, Sara[1, 2] ; Sallée, Jean-Baptiste[1, 3] ; Fraser, Alexander D.[4, 5] ; Massom, Robert A.[5, 6] ; Reid, Phillip[7] ; Sumner, Michael[6] ; Guinet, Christophe[8] ; Harcourt, Robert[9] ; McMahon, Clive[2, 9, 10]; Bailleul, Frédéric[11]; Hindell, Mark A.[2, 5]; Charrassin, Jean-Benoit[1].

(1) Sorbonne Universités, UPMC Univ., Paris 06, UMR 7159 CNRS-IRD-MNHN, LOCEAN-IPSL, 75005 Paris, France

(2) Marine Predator Unit, Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart, Tasmania 7001, Australia

(3) British Antarctic Survey, High Cross, Cambridge, CB3 0ET, UK

(4) Institute of Low Temperature Science, Hokkaido University, N19 W8, Kita-ku, Sapporo, Japan 060-0819

(5) Antarctic Climate & Ecosystems Cooperative Research Centre, University of Tasmania, Private Bag 80, Hobart, Tasmania 7001, Australia

(6) Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia

(7) Australian Bureau of Meteorology, Centre for Australian Weather and Climate Research, Hobart, Tasmania 7001, Australia

(8) Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372 Université de la Rochelle-CNRS, 79360 Villiers en Bois, France

(9) Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia

(10) Sydney Institute of Marine Science, 19 Chowder Bay Road, Mosman, New South Wales 2088, Australia

(11) South Australian Research & Development Institute (SARDI), 2 Hamra Avenue, West Beach, South Australia 5024

Highlights

- Unveil linkages between foraging trips of 46 southern elephant seals and sea ice
- Females follow the seasonal ice edge extent; males remain on the continental shelf
- Females exploit the under-ice ecosystem by foraging below high concentration sea ice
- Males favour the least concentrated sea ice, probably in coastal polynyas and leads
- High variability of sea ice around the seals is key to relax its breathing constraint

Abstract

Investigating ecological relationships between predators and their environment is essential to understand the response of marine ecosystems to climate variability and change. This is particularly true in polar regions, where sea ice (a sensitive climate variable) plays a crucial yet highly dynamic and variable role in how it influences the whole marine ecosystem, from phytoplankton to top predators. For mesopredators such as seals, sea ice both supports a rich (under-ice) food resource, access to which depends on local to regional coverage and conditions. Here, we investigate sex-specific relationships between the foraging strategies of southern elephant seals (*Mirounga leonina*) in winter and spatio-temporal variability in sea ice concentration (SIC) and coverage in East Antarctica**.** We satellite-tracked 46 individuals undertaking post-moult trips in winter from Kerguelen Islands to the peri-Antarctic shelf between 2004 and 2014. These data indicate distinct general patterns of sea ice usage: while females tended to follow the sea ice edge as it extended northward, the males remained on the continental

ACCEPTED MANUSCRIPT

shelf despite increasing sea ice. Seal hunting time, a proxy of foraging activity inferred from the diving behaviour, was longer for females in late autumn in the outer part of the pack ice, ~150 - 370 km south of the ice edge. Within persistent regions of compact sea ice, females had a longer foraging activity (i) in the highest sea ice concentration at their position, but (ii) their foraging activity was longer when there were more patches of low concentration sea ice around their position (either in time or in space; 30 days & 50km). The high spatio-temporal variability of sea ice around female positions is probably a key factor allowing them to exploit these concentrated patches. Despite lack of information on prey availability, females may exploit mesopelagic finfishes and squids that concentrate near the ice-water interface or within the water column (from diurnal vertical migration) in the pack ice region, likely attracted by an ice algal autumn bloom that sustains an under-ice ecosystem. In contrast, male foraging effort increased when they remained deep within the sea ice (420 - 960 km from the ice edge) over the shelf. Males had a longer foraging activity (i) in the lowest sea ice concentration at their position, and (ii) when there were more patches of low concentration sea ice around their position (either in time or in space; 30 days & 50km) presumably in polynyas or flaw leads between land fast and pack ice. This provides access to zones of enhanced resources in autumn or in early spring such as polynyas, the Antarctic shelf and slope. Our results suggest that some seals utilized a highly sea ice covered environment, which is key for their foraging effort, sustaining or concentrating resources during winter.

1. Introduction

In recent decades, complex regional patterns of change have occurred in both the seasonality and extent of sea ice around Antarctica (Parkinson and Cavalieri, 2012; Stammerjohn et al., 2012), widely affecting the dependent Antarctic marine ecosystem (Massom and Stammerjohn, 2010). For predators, recent studies have highlighted clear relationships between population dynamics and broad-scale changes and inter-annual variability in sea ice concentration and extent – for both "sea ice obligate" seabird and seal species (e.g. Barbraud and Weimerskirch, 2001, 2006; Proffitt et al., 2007; Siniff et al., 2008; Massom et al., 2009; Forcada et al., 2012; Jenouvrier et al., 2012) and "non sea ice obligate" species such as chinstrap penguins (*Pygoscelis Antarctica*, Trivelpiece et al., 2011) and southern elephant seals (*Mirounga leonina*, Siniff et al., 2008; van den Hoff et al., 2014). However, populations have not responded in a uniform way around Antarctica, and contrasting trends are observed that reflect regional differences in climate-induced changes in sea ice properties and in species ecology and biological requirements (Massom and Stammerjohn, 2010; Constable et al., 2014; Southwell et al., 2015). Many studies exploring the links between sea ice changes and seals focused on the Bellingshausen and Amundsen seas sectors (e.g. Siniff et al., 2008; Forcada et al., 2012) or the Ross sea sector (e.g. Proffitt et al., 2007; Ainley et al., 2015) where strongly opposing trends in the extent and the seasonality of the regional sea ice, were observed (Stammerjohn et al., 2008). However, studies in East Antarctica where patterns of sea ice change and variability are quite complex, comprising mixed signals on regional scales (Massom et al., 2013), are lacking for marine mammals (Weimerskirch et al., 2003). A major current challenge involves establishing a better mechanistic understanding of the linkages between climate, sea ice and lower to upper trophic levels in the high-latitude Southern Ocean (Ducklow et al., 2007). Such information is crucial to allow better prediction of the future response of Antarctic predators to climate change and variability. Finally, while population demographic studies are essential when considering the links between sea ice and marine

ACCEPTED MANUSCRIPT

predators (e.g. in East Antarctica, Barbraud and Weimerskirch, 2001, 2006; Jenouvrier et al., 2012), they may not in themselves be sufficient to understand the precise nature of the linkages at play; inclusion of information of at-sea foraging behaviour relative to sea ice habitat is also necessary.

For seals, the ice supports a rich (under-ice) food resource because it provides both a substrate for the growth of ice algae and a refuge for herbivorous zooplankton such as juvenile krill and other crustaceans (Marschall, 1988; Flores et al., 2011, 2012b; David et al., 2016), which in turn attracts upper trophic levels such as pelagic fish and their predators (Eicken 1992; van Franeker et al., 1997; Reid and Croxall, 2001; Brierley and Thomas, 2002; Ainley et al., 2010b; Fraser & Hofmann, 2003). The access to under-ice food resource depends on local to regional sea ice coverage and conditions (Ainley et al., 2010b), thus there is a fine balance between sea ice being either beneficial as it provides access to a rich food source or an impediment for air-breathing marine predators, because of the physical barrier it builds between the ocean and air. The marginal ice zone was also found to be biologically active with concentration of krill, fishes and predators throughout the year (Lancraft et al., 1991; Bost et al., 2004). However, it is unknown which types of sea ice habitat are most used by deep-diving predators such as southern elephant seals, how they might benefit from the under-ice resources, and how they might overcome the physical constraints associated with the presence of sea ice.

In this study, we combine animal telemetry (i.e. tracks and diving behaviour) and satellite-derived ice concentration data acquired over the different years covering the telemetry study period, with statistical modeling to analyse the interaction with, and reliance on, sea ice characteristics of a "non sea ice obligate" species – the southern elephant seal (SES). Specifically, we investigate the movements (horizontal and vertical) and foraging activity of SESs from the Kerguelen Islands as a function of gender and intra-seasonal variability in East Antarctic sea ice habitat, defined here by sea ice concentration, extent and spatio-temporal variability. While sea ice concentration and extent are critical to Antarctic ecosystems through a possible cascading effect from krill to upper predators (Loeb et al., 1997; Nicol et al., 2000; Brierley and Thomas, 2002; Fraser & Hofmann, 2003; Atkinson et al., 2004; reviewed by Flores et al., 2012a), the spatio-temporal variability of sea ice concentration gives important information on the capacity of a sea ice environment to sustain active under-ice ecosystems (Eicken 1992; Brierley and Thomas, 2002; Ainley et al., 2010b; Nicol, 2006; Clarke et al 2008; Bluhm et al., 2010), and on the extent to which sea ice is a constraint for air breathing predators.

Although considered to be "non sea ice obligate", some SESs interact strongly with the sea ice environment during their long annual migrations from their breeding colonies on sub-Antarctic islands to their high-latitude foraging grounds (Bornemann et al., 2000; Bailleul et al., 2007; Biuw et al., 2010; Hindell et al., 2016; Labrousse et al., 2015). Importantly for this study, there are two foraging strategies during the post-moult foraging trips of SESs from Kerguelen Islands; some individuals use the Kerguelen shelf or frontal regions of the Antarctic Circumpolar Current (ACC), while others travel south within sea ice covered areas to reach the peri-Antarctic shelf (Bailleul et al., 2010). Moreover, as deep-diving, wide-ranging mesopredators (Hindell et al.,1991a, 1991b; McConnell et al., 1992) and major consumers of marine resources of the Southern Ocean (Guinet et al. 1996, Hindell et al. 2003), SESs depend upon an extensive set of trophic levels within the marine food web and their foraging and breeding performances reflect ecosystem status (Trathan et al., 2007). They also utilize different marine habitats depending on their sex (Bailleul et al., 2010; Labrousse et al., 2015) and breeding colony location (Biuw et al., 2007; Hindell et al., 2016). Among the main populations located in the South Atlantic, Southern Indian and South Pacific Oceans, contrasting demographic trends are observed,

ACCEPTED MANUSCRIPT

presumably in response to environmental variability (McMahon et al., 2005; Hindell et al., 2016). Studying how the environment will modulate the availability of resources for a demographically stable population, such as the Kerguelen Islands population, is essential to use to compare with and help to understand the increasing or decreasing trends observed in the other populations.

This study follows on from previous work on Kerguelen SESs during winter, showing that adult females were closely associated within the marginal sea ice zone, following the northward sea ice extension, and foraging in highly concentrated sea ice close to the sea ice edge (Bailleul et al., 2007; Hindell et al., 2016; Labrousse et al., 2015). In contrast, it was shown that sub-adult males remained deep within the sea ice foraging mainly over the Antarctic shelf or within the Antarctic Slope Front (ASF) in sea ice of intermediate concentration. The pattern of males diving in waters with low sea ice concentration while on the Antarctic shelf could be explained by either an early arrival in the season in the Antarctic region, movements restricted to sectors where sea ice extent is low, or potentially by use of coastal polynyas (Bailleul et al., 2007; Hindell et al., 2016; Labrousse et al., 2015). This study builds upon this previous work by investigating sea ice habitat use using both sea ice concentration and for the first time the spatio-temporal variability of sea ice around the seals' position using a long (i.e. 7 years) and consistent time-series of male and female SESs tracking data. We investigated both the habitat encountered along their tracks and the foraging habitat. However, unlike previous studies we took into account (in each of those linkages) the seals' relative distance from the sea ice edge in an attempt to precisely define the change of sea ice conditions according to the seal movements in the sea ice zone. Finally, we investigated the seasonality of foraging activity when males and females were in the sea ice zone, which has not been previously reported in other studies.

2. Material and methods

2.1 Animal handling, deployment, data collection and filtering

In this study, we use positional and dive pressure data from a total of 46 post-moulting SESs (23 females and 23 sub-adult males) that were captured and instrumented with CTD-SRDLs (Sea Mammal Research Unit, University of St Andrews) between December and February in 2004, 2008-2009 and 2011-2014 on the Kerguelen Islands (49°20'S, 70°20'E) (details in Appendix A, Table A1). These animals were chosen from the larger dataset because they visited the area south of 55°S, which is equivalent to the maximum latitude of annual sea ice extent (in September). Unusual behaviour was observed with five animals (two females and three males) returning to the colony before heading back to sea again. For these individuals, the section of tracks where animals travelled again south within the sea ice region (one female and two males) after their return to the colony were removed from analysis. Details of the instrumentation, seal handling and data processing for filtering ARGOS positions are provided by Labrousse et al. (2015). An average of 18.1 ± 8.6 tag positions were transmitted via the ARGOS system each day. Tags were programmed to record dive depth and time every 4s, from which start time, end time, duration and post-dive surface interval were determined for individual dives. Four time-depth points were transmitted for each dive and were determined by a broken-stick algorithm that selects the largest inflection points in the fine scale trajectory of depth as monitored by the tag every 4 sec (Sea Mammal Research Unit). A zero offset surface correction was set to 15 m (Guinet et al., 2014). An average

ACCEPTED MANUSCRIPT

weight of 307 ± 52 kg and 559 ± 244 kg, and an average length of 245 ± 13 cm and 293 ± 39 cm were observed for females and males respectively.

2.2 Sea ice parameters

As in Labrousse et al. (2015), daily estimates of sea ice concentration were derived from satellite Advanced Microwave Scanning Radiometer (AMSR) data at 6.25 km resolution (University of Bremen, http://www.iup.physik.uni-bremen.de:8084/amsr/amsre.html). The data gap for the change from AMSR-E to AMSR-2 in 2012 was filled by data from the Special Sensor Microwave Imager/Sounder (SSMI/S) satellite instrument to provide a consistent and continuous time-series of daily Antarctic sea ice maps from 2004-2014. Although the SSMI/S observations used for 2012 were provided at a lower resolution (12.5 km) than the AMSR observations, the same sea ice concentration algorithm was applied and the grid spacing of 6.25 km was kept for consistency in our analysis.

The distance of seals from the sea ice edge was calculated as the minimum distance between seal positions and the sea ice edge contour, as defined by the 15% sea ice concentration isoline (following Stammerjohn and Smith, 1997). Contours corresponding to outlying floes or polynyas were removed to prevent bias in our sea ice edge distance computation.

Two variables representing the spatio-temporal variability of sea ice around the seal's position were investigated, assuming that sea ice becomes a constraint when the concentration is high. These are: (i) the area covered by sea ice with a concentration of >80% within a 50 km radius around the animal ($\mathcal{A}_{80\%}$; as a measure of the spatial variability of concentrated sea ice patches); and (ii) the number of days with a sea ice concentration of >80% at a given location within a 30 day window ($\mathcal{T}_{80\%}$; as a measure of the time variability of concentrated sea ice patches). A schema illustrating these two variables is shown in Figure 1.

Finally, the spatial variability of concentrated patches ($\mathcal{A}_{80\%}$) showed a strong seasonal signal from March to August-September. Thus, we computed the anomaly of the spatial variability from its seasonal cycle (denoted $\mathcal{A}'_{80\%}$; Appendix B). It consisted of (i) computing the median of the observations from the time-series of $\mathcal{A}_{80\%}$ for males and females (Appendix B, Figure B1A – B), (ii) removing this median from each observation to obtain the anomaly of the spatial variability from its seasonal cycle (hereafter denoted $\mathcal{A}'_{80\%}$; Appendix B).

2.3 Proxy of foraging activity

Foraging activity of each SES was analysed at the dive scale using the methodology developed by Heerah et al. (2015), which estimates the time spent in segments with low vertical velocities (i.e. "hunting time"; vertical speed <= 0.4 $m.s^{-1}$). This time spent at low vertical velocity has been shown to capture most of prey capture events in a separate validation study (i.e. hunting time segments were associated with 68% of all prey capture events inferred from acceleration data; Heerah et al., 2015). In the present study, a long hunting time within a dive does not necessarily mean foraging success or high prey availability, but enhanced foraging activity occurring during the dive. Heerah et al. (2015) found that segments with "hunting time" were associated with four times more prey capture attempts than other segments.

2.4 Statistical modelling of the influence of sea ice parameters on foraging activity

ACCEPTED MANUSCRIPT

Linear mixed effects models (LMMs) were fitted to examine the statistical relationships between seal foraging activity (expressed by the hunting time per dive) and sea ice concentration, its spatial and temporal variability ($\mathcal{A}_{80\%}$ and $\mathcal{T}_{80\%}$) taking into account the influence of the season (expressed by the day of year). The different steps of the statistical approach are summarized in Figure 2. The distance of seals from the sea ice edge within the ice was binned in 6 quantiles for females and males using the R package Hmisc (from R Development Core Team, function *cut2*). This variable was then added as an interaction term for all variables. Given the different behaviour of males and females, we constructed a model for each sex. A subset of the data was extracted to only focus on parts of the tracks influenced by sea ice; for this, only positions inside the sea ice and from March (when the seasonal signal of sea ice concentration starts to increase; cf. Appendix C, Fig. C1) to the end of the post-moult trip were used for subsequent analysis. Models were computed with the R package nlme (from R Development Core Team, function *lme*; Pinheiro et al., 2015) using restricted maximum likelihood. The hunting time per dive (i.e. response variable) was centred and scaled for each seal prior to analysis to correct for non-Gaussian distribution. Outliers, homogeneity and collinearity in the variables were checked following Zuur et al. (2010). Season was highly correlated to $\mathcal{A}_{80\%}$ (the later in the season, the higher was $\mathcal{A}_{80\%}$), so we did not consider both $\mathcal{A}_{80\%}$ and the season in a single model. To disentangle the effect of the season from the effect of $\mathcal{A}_{80\%}$, we constructed three different model suites for each sex: (i) including $\mathcal{A}_{80\%}$ but without the season (Fig. 2, model 1), (ii) including the season but without $\mathcal{A}_{80\%}$ (Fig. 2, model 2) and (iii) including the anomaly of the spatial variability from its seasonal cycle (hereafter denoted $\mathcal{A}'_{80\%}$: Appendix B), (Fig. B2, model 3). We present below the model suite (1) including all the sea ice variables, while the two other model suites are presented in Appendix D. Among the different variables (SIC, $\mathcal{A}_{80\%}$, and $\mathcal{T}_{80\%}$, and the position of seals within sea ice), some collinearities were observed however we did not remove any variables because of likely independent effects on hunting time (Freckleton et al., 2011). Explanatory variables were standardized (centered and scaled) to facilitate model convergence and to allow comparisons of the respective contributions of the predictors.

Model selection again followed Zuur et al. (2010). We first determined the optimal structure of each model by assessing the full model with fixed effects and their interaction term with and without individual seals as a random intercept term to ensure that this term contributed to the model fit. We then assessed the effect of including an autocorrelation term in the resulting optimal model by using the AR-1 autocorrelation (corAR1) argument. Finally, we tested the individual fixed and interaction terms by sequentially removing the least non-significant terms from the model. Model selection was made using the likelihood ratio test, based on maximum likelihood (ML). Terms were only retained if they improved the fit ($p < 0.05$; Zuur et al., 2009; Bestley et al., 2010). In all cases, models were ranked via Akaike Information Criterion (AIC) (Burnham and Anderson, 2002), to ensure that the most parsimonious (i.e. lowest AIC value) model was selected. The final model was then fitted using restricted maximum likelihood (REML). All variables were retained in each model. The interaction term corresponding to the distance of the animal from the sea ice edge was also retained in each model, suggesting that the relationship between hunting time and sea ice patterns was influenced by the position of the animal within sea ice at the dive scale.

Model validations were checked by plotting Pearson residuals against fitted values, and against each explanatory variable, verifying homogeneity and normality of residuals (Zuur et al., 2010). Finally, a marginal R-squared (i.e. variance explained by fixed factors only) and a conditional R-Squared (i.e. variance explained by both fixed and random factors) were calculated as described in Nakagawa and Schielzeth (2010; 2013).

ACCEPTED MANUSCRIPT

3. Results

Data from a total of 286,843 dives were collected for 23 females and 23 males from 2004 to 2014. The combined migration tracks from the Kerguelen Islands in the seasonal sea ice zone are shown in Figure 3, and statistics and information on each seal are given in Table A1 (Appendix A). Collation of this information shows a number of gender-specific patterns in relation to their travel to and from, and time and behaviour within, the sea ice zone. Among the 46 individuals from 2004 to 2014, five individuals (four females and one male) did not go into the sea ice: two arrived on the shelf early in the season and left before sea ice formed, two lost their tag, had tag failures or died before they reached sea ice and the last individual did not go enough southwards to reach sea ice. These five seals were removed from subsequent analyses and the study was therefore based on 41 individuals. Males and females left the colony between late December and early March. Females returned to the colony between September and October, and males between September and November (data from animals with active tag transmission, from their departure until return to the colony, 7 females and 8 males). Females travelled 35 ± 28 km per day, and males 32 ± 35 km per day, however when seals were within sea ice, females travelled 24 ± 18 km per day and males 17 ± 18 km per day.

Males, on average, remained further within sea ice (337 ± 267 km from the sea ice edge; maximum 962 km) than females (128 ± 195 km from the sea ice edge; maximum 745 km). Both sexes were the furthest within the sea ice zone during the months of May, June and July. The cumulative number of dives of male and female SESs relative to the sea ice extent and their distance from the sea ice edge is shown on Figure 4. While females tended to follow the sea ice edge as it moved northward (Fig. 4A) males remained mostly on the continental shelf (Fig. 4B). In these environments, the habitat available to seals and male and female preferences in terms of sea ice concentration are shown in Figure 5. Both males and females used all ranges of sea ice concentration but their habitat differed from the habitat available (Fig. 5), indicating potential preferences and choices made by the animals.

The cumulative dive durations of male and female SESs relative to the 3 sea ice parameters and seal distance from the sea ice edge are shown on Figure 6. Close to the sea ice edge, both sexes strongly favoured the highest sea ice concentration (90 – 100 % concentration; Fig. 6A, B). This tendency was clearer for females than for males, and even clearer for females moving deeper into the sea ice zone (i.e., 100 – 200 km from the ice edge; Fig. 6B). Males, on the other hand, remained mostly on the continental shelf in regions of less concentrated sea ice i.e., coastal polynyas (Fig. 6A).

On average (± one standard deviation), 37 ± 14 dives per day were collected for females, and 41 ± 19 dives per day for males. For positions only inside the sea ice and from March, the mean time spent hunting per dive was 17 ± 11 min for females and 13 ± 10 min for males. The further poleward the seals were from the sea ice edge (per class of distance), the shallower their maximal diving depths i.e., from 446 ± 194 m to 347 ± 212 m for females and from 381 ± 215 m to 247 ± 176 m for males (Appendix E, Fig. E1-A, B). However, high individual variability does not allow us to conclude about the significance of the relationship between diving depths and the distance from the sea ice edge. Moreover, a southward decrease in dive depth may simply reflect the fact that the bottom topography becomes shallower on the shelf (Appendix E, Fig. E1-C, D), so we cannot conclude about the influence of the distance from the sea ice edge on seal diving depth.

ACCEPTED MANUSCRIPT

Within the sea ice region, 39 individuals (of the 46) performed some shallow dives (i.e. shallower than 40 m) representing 10 ± 6% of the total dives for males and 4 ± 5 % for females (Appendix A, Table 1). For this specific diving behaviour, geographic repartition, frequency of distribution relative to the time of day and their characteristics in terms of sea ice concentration and distance from the sea ice edge are detailed in Figure 7. Interestingly, 72% of these dives happen during the night (solar angle <= -6°) compared to daylight (solar angle => 0) and twilight (-6° < solar angle < 0). These dives were often close to the coast, among sea ice concentration of 92 ± 19% and 83 ± 25% for females and males respectively (Fig. 7) and at 133 ± 134 km and 258 ± 219 km from the sea ice edge for females and males respectively. It is the first time such specific behaviour under sea ice has been reported for SESs.

3.1 Influence of sea ice variability on SESs movements

Close to the sea ice edge (from 0 to 100 km), females spent most of their time in transient patches of sea ice ($\mathcal{T}_{80\%}$ ~ 10–15 days per month; Fig. 6D) while males dived intensively in patches of both low and high sea ice persistence (low and high values of $\mathcal{T}_{80\%}$; Fig. 6C). Females exploited a wide range of $\mathcal{A}_{80\%}$, spanning both regions of spatially compact sea ice (up to $\mathcal{A}_{80\%}$ of 80 %) and very sparsely covered by compact sea ice ($\mathcal{A}_{80\%}$ of less than 25%; Fig. 6F). Males mostly remained in regions sparsely covered by compact sea ice ($\mathcal{A}_{80\%}$ of less than 25%; Fig. 6E).

Further investigation into the characteristics of high sea ice concentration sectors in which seals foraged reveals distinct differences. For instance, when females were into the pack (100 – 200 km from the ice edge), they encountered persistent and spatially compact sea ice i.e., $\mathcal{T}_{80\%}$ ~ 25 – 30 days per month (Fig. 6D) and $\mathcal{A}_{80\%}$ ~ 30 – 70 % (Fig. 6F). In contrast, areas of concentrated sea ice encountered by males were more transient (i.e. low $\mathcal{T}_{80\%}$; Fig. 6C) but still relatively compact spatially ($\mathcal{A}_{80\%}$ ~ 30 – 70 %; Fig. 6E).

Inside the sea ice zone (>100 km from the sea ice edge), both male and female dives tended to be associated with spatially compact sea ice covered areas (high values of $\mathcal{A}_{80\%}$). However, $\mathcal{A}_{80\%}$ had a strong seasonal signal, increasing steadily from summer to winter (Appendix B) and probably associated with the seasonal increase in sea ice concentration (the larger the sea ice concentration, the larger is $\mathcal{A}_{80\%}$). This raises the following question: do seals really favour high values of $\mathcal{A}_{80\%}$ (i.e. spatially compact sea ice patches) among regions of more or less spatially compact sea ice patches or do our results only reflect seals entering in the pack later in the season, when $\mathcal{A}_{80\%}$ is high everywhere? To address this question in the following section, one has to consider the sea ice characteristics available to seals. We did this by considering different statistical models, and by seeking to statistically quantify how sea ice characteristics relate to seal hunting time.

3.2 Quantifying the influence of sea ice patterns on SESs foraging activity

A total of 41 individuals (19 females, 22 males) and of 84,964 dives (36,177 for females; 48,787 for males) was used to build the two models. Model results are shown in Table 1 and Figure 8; they were divided in different ranges of distance from the sea ice edge. For each variable considered in the model, we present the data that was used to produce the model in each of these ranges (Fig. 8C, D: boxplots for sea ice concentration; Fig. 8G, H: boxplots for $\mathcal{T}_{80\%}$; Fig. 8K, L: boxplots for $\mathcal{A}_{80\%}$) and the regression lines fitted by the model (Fig. 8A, B: sea ice concentration; Fig. 8E, F: $\mathcal{T}_{80\%}$; Fig. 8K, L: $\mathcal{A}_{80\%}$). Finally, the influence of the interaction term (i.e. distance of seal from the sea ice edge) on the hunting time is described in Fig. 8M, N.

ACCEPTED MANUSCRIPT

3.2.1 Summary of model statistics

Both males and females had a longer hunting time when further inside sea ice within their respective regions: males hunted longer closer to the Antarctic continent (i.e. presumably in polynyas or in leads at the fast ice boundary) and females further away from the sea ice edge in the outer part of the pack ice. Habitat use and the relationship between hunting time per dive and sea ice patterns within these sectors are summarized on the diagram Figure 9. At a given position, females had a longer hunting time in concentrated sea ice while males used low sea ice concentration. Both males and females had a longer hunting time during the autumn season and high spatio-temporal variability of sea ice around their positions (low $\mathcal{T}_{80\%}$ and low $\mathcal{A}'_{80\%}$) positively influenced their hunting time (Fig. 9).

3.2.2 Model statistics for males and females

Hunting time increased for males deep within the pack and fast ice (420 - 960 km from the edge) over the shelf (Fig. 8M) and for females when they were further than 150 km from the edge into the pack (Fig. 8N).

Sea ice concentration had a negative influence on male hunting time and this negative influence was greater when males were deeper in the sea ice zone (Fig. 8A). In contrast, female hunting time was positively correlated with sea ice concentration further than 30 km from the sea ice edge. In these regions, females were in high sea ice concentrations (Fig. 8D) where they favored the highest sea ice concentration available for hunting (Fig. 8B).

Males favoured the low values of $\mathcal{T}_{80\%}$ for hunting (Fig. 8E), even though they had access to a wide range of different regimes of low to high values of $\mathcal{T}_{80\%}$ (Fig. 8G). In contrast, females had access to only relatively high values of $\mathcal{T}_{80\%}$ further than 30 km from the edge (Fig. 8H), but like male behaviour, females favored the low values of $\mathcal{T}_{80\%}$ (Fig. 8F).

Interestingly, male and female hunting time was always longer for high values of $\mathcal{A}_{80\%}$ (Fig. 8I, J). However, as noted above $\mathcal{A}_{80\%}$ is correlated with the season, so it is unclear if this result is an indication of seals favouring high values of $\mathcal{A}_{80\%}$, or if it reflects seals hunting longer later in the season for other reasons. Given their correlation (r ~ 0.8), it is impossible to clearly disentangle the influence of the two parameters. However, we repeated the same statistical models while removing the seasonal cycle to $\mathcal{A}_{80\%}$. For a given time of year, hunting was shorter when $\mathcal{A}'_{80\%}$ increased (Appendix D, Fig. D2-I, J, K, L). One interpretation would be that hunting time is longer later in the season, but for a given season, it is even longer if seals find patches of sea ice more sparsely distributed (low $\mathcal{A}_{80\%}$).

Consistent with this, the statistical model considering season without $\mathcal{A}_{80\%}$, indicated that hunting time increased with the day of year (Fig. D1-I, J). However, for males this relationship between hunting time and day of year became close to zero when males were further into the pack, i.e. later in the season from about July onward (Fig. D1-I and D1-K). Therefore, these results suggested that hunting time increased for males and females with the day of year from about April (day of year 90) to June (day of year 180). For males we found that the relationship with hunting time was lower with day of year from July (day of year 180) to October (day of year 270), suggesting seasonal variability with enhanced foraging conditions in austral autumn/early winter. For females, the lack of observations after July precludes evidence of a reversal after autumn.

ACCEPTED MANUSCRIPT

Models that included season (Appendix D, Fig. D1) or $\mathcal{A}_{80\%}$ (Fig. 9) explained 30% and ~20 % of the variance respectively (conditional R^2). However, when seasonal cycle of $\mathcal{A}_{80\%}$ was removed, the explained variance of the models dropped to 6 - 14% (conditional R^2 for females and males respectively; Appendix D, Fig. D2). This points to the importance of seasonal variability; either the season itself or seasonally variable quantities, such as $\mathcal{A}_{80\%}$.

4. Discussion

In the present study, we chose to elaborate on the potential attractiveness of under-ice ecosystems for SESs in terms of resources to explain the strategy adopted by some individuals to forage within sea ice covered areas as opposed to those foraging in the vicinity of the Kerguelen Plateau in frontal zones. However, it is important to note that travelling south within sea ice covered areas may also be an avoidance response of predation by sub-Antarctic killer whales inhabiting the vicinity of the Kerguelen Plateau (Pitman, 2011). Further research is needed to measure the killer whale predation on SESs foraging in open waters versus in the sea ice zone, for example using life-history transmitters (Horning and Mellish 2009), in order to quantify the survival advantage that sea ice as an anti-predation refuge may confer to SESs.

Sea ice characteristics influence foraging behaviour of male and female Kerguelen elephant seals, in markedly distinct ways; here we confirmed the results observed in Bailleul et al. (2007), Hindell et al. (2016) and Labrousse et al. (2015). We also brought new insights by defining male and female habitat based on their distance from the sea ice edge and by quantifying the relation between foraging activity and sea ice concentration given their distance from the sea ice edge. While females tended to remain within 200 km of the sea ice edge (within pack ice) and foraged most intensively in high concentrations of sea ice (see example of tracks in Fig. 10), males tended to remain on the continental shelf (presumably in polynyas or leads at the fast ice boundary), foraging in low sea ice concentrations (see example of tracks in Fig. 11).

Hindell et al. (2016) described the change in broad-scale habitat use of Kerguelen post-moult SESs throughout the year, with females moving northwards with the growth of the winter sea ice, and males remaining over the shelf. However, our study is the first to quantify the seasonality in foraging activity (in terms of time spent “hunting” during a dive) throughout winter. There was a clear increase in foraging activity for both males and females with a peak in later autumn/early winter and this will be discussed later.

For the first time, we investigated the importance of the spatio-temporal variability of sea ice during SES foraging trips, which is a key factor enabling them to exploit these ice covered regions, as suggested in Labrousse et al. (2015). Acting as an ecological double-edged sword, sea ice provides and concentrates a rich ecosystem during wintertime, while also potentially representing a physical barrier for air breathing predators (Chambert et al., 2015). Several studies based on emperor penguin already suggested an optimum level of ice cover with neither complete absence of sea ice nor heavy and persistent sea ice providing satisfactory conditions for sea ice dwelling species (Ainley et al., 2010a; Barbraud et al., 2012; Jenouvrier et al., 2012). Moreover, the regionally complex patterns in sea ice trends observed in East Antarctica over the past 30 years with local variability of the marine “icescape” (Massom et al., 2013) might allow the SES Kerguelen population to exploit concentrated sea ice patches within pack ice or to remain deep into the sea ice zone in polynya areas. This contrasts with Macquarie Island where increasing sea ice extents in the western Ross Sea sector were negatively

ACCEPTED MANUSCRIPT

correlated with the number of breeding female SESs (with a lag of 3 years) presumably by limiting the access to profitable prey patches (van den Hoff et al., 2014).

The gender difference in the foraging areas visited is presumably in part explained by differences in energy requirements between sub-adult males and adult females and the distribution of their prey (Bailleul et al., 2007). Small, schooling prey (e.g. Myctophids; Cherel et al., 2008) were likely to be targeted by seals foraging in pelagic waters (i.e. mainly females), larger prey items such as Nototheniids, Morids (Bradshaw et al., 2003; Banks et al., 2014) are probably more dominant prey items for seals foraging on the shelf (i.e. mainly males). However, a mix of finfish (Myctophids, Nototheniids), squid and krill is probably found in the diet of seals foraging in the pack ice region outside the shelf, i.e. mainly females, (Banks et al., 2014; Walters et al., 2014).

The difference in the foraging areas visited between sexes can also be explained by the timings of migration to and from the high latitudes; males in general arrive earlier than females on the shelf before sea ice forms probably allowing them to reach these remote areas without being constrained by sea ice. Moreover, because the males studied were sub-adult males, they may not prioritize returning to the colony for breeding because they were not sexually mature and thus they were able to stay longer within the sea ice region. In contrast females arrive later when sea ice is already formed and leave earlier as they may prioritize returning to the colony to give birth. Thus females might avoid being trapped by sea ice by foraging in the pack but by following the sea ice edge (Bailleul et al., 2007; Hindell et al., 2016; Labrousse et al., 2015).

Understanding these patterns requires also consideration of the resources available to the animals. We do this below in the context of different sea ice zones, which might aggregate specific resources, as well as in the framework of the seasonal cycle in ice and primary production.

4.1 Sea ice zones and associated resources

In East Antarctica, the sea ice cover is made up of three zones with distinct characteristics (Massom and Stammerjohn, 2010). These are (from north to south): i) the highly-dynamic “marginal ice zone” (MIZ), which typically extends 100 km or so south from the ice edge, and is generally made up of small floes and diffuse ice conditions (depending on wind direction); ii) the “inner pack ice” zone (PIZ) comprising larger floes separated by leads; and iii) a coastal zone comprising the band of compact “landfast (fast) ice” (FIZ) and persistent and recurrent areas of low-concentration sea ice in the form of polynyas and flaw leads. Females in our study mostly remained and foraged in the MIZ and the outer part of the pack ice, while males used all three sea ice zones. Below, we summarise female and male foraging behaviour in each of these zones in more detail.

4.1.1 Male and female foraging behaviour in the MIZ

Within the MIZ, both females and males encountered regions characterized by (i) relatively low to intermediate sea ice concentration; (ii) low $\mathcal{T}_{80\%}$; and (iii) low to high $\mathcal{A}_{80\%}$. The MIZ is characterized by high sea ice variability in time and space and enhanced biological activity due to sea ice melt and breakdown releasing an important quantity of food resources (i.e. ice algae) under a strong influence of wind action and ocean wave-ice interaction processes (Wadhams, 2000; Massom et al., 2006; Karnovsky et al., 2007; Squire, 2007; Massom and Stammerjohn, 2010). However, it is not in this region that seals had the longest hunting times per dive.

4.1.2 Female foraging behaviour in the PIZ

Within the PIZ, females mostly remained in the outer part of the pack (150 – 370 km away from the edge) and had their longest hunting times there compared to the MIZ. Within this region, generally characterized

ACCEPTED MANUSCRIPT

by persistent and compact sea ice, females foraged most intensively (i.e. longer hunting times) (i) in the highest sea ice concentration at their position, but (ii) their hunting time was longer in areas of low concentration sea ice around their position (either in time or in space; 30 days & 50km). The spatio-temporal variability of sea ice around female positions probably allowed them to exploit concentrated patches of prey without being trapped by the ice (Raymond et al., 2015). Heerah et al. (2016) observed similar results with Weddell seals hunting longer in more concentrated sea ice in regions with variable sea ice (e.g. Davis station) compared with areas where sea ice conditions were persistent and less variable (e.g. Dumont d'Urville), where the contrary was observed.

Despite a lack of information on prey, females are known to have a multi-species diet, (i.e. mix of finfish and squid) in the pack-ice habitat compared with shelf and pelagic habitats where females have a higher proportion of finfish (Banks et al., 2014). The study of Flores et al. (2008) provided evidence of a second major trophic pathway from phytoplankton to mesopredators in the pack ice region during autumn, via copepods and myctophids, comprising intermediate trophic steps via cephalopods and large finfishes. In high Antarctic pelagic waters, about 24 to 70 % of the biomass of the myctophid *Electrona antarctica* from 0-1000 m depth, was found to occur in the upper 200 m at night (Lancraft et al., 1989; Donnelly et al., 2006) and it was reported by Kaufmann et al. (1995) that mesopelagic organisms migrate closer to the surface beneath pack ice than in open water. Thus, concentration and/or availability of resources in the pack ice region near the ice-water interface or within the water column (from diurnal vertical migration) possibly makes it physiologically more rewarding to forage under-ice compared to the deep dives necessary to catch Myctophids in open waters or compared to the risk of being trapped by sea ice by foraging on Notothenioids (Bradshaw et al., 2003) in densely sea ice covered shelf regions. Unfortunately, there is so far only anecdotal evidence that important prey species of SESs are found in the ice-water interface layer, such as squid and finfish (Ainley et al., 1986, Kaufmann et al. 1995, Flores et al. 2011, David et al. 2016).

4.1.3 Male foraging behaviour in the PIZ and FIZ

The pack ice region for males represents both a transit and a feeding area. However, male hunting time was longer in regions close to the Antarctic coast, in the southern part of the pack and fast ice (420 - 960 km away from the edge). Within this environment, they foraged most intensively (i.e. longer hunting times) (i) in the lowest sea ice concentration at their position, and (ii) when there were more patches of low concentrated sea ice around their position (either in time or in space; 30 days & 50km) likely to be associated with polynyas, or recurrent flaw leads separating persistent fast ice from moving pack ice (Massom and Stammerjohn, 2010). In addition to relieving the sea ice constraint, these open water areas can sustain high biological activity in spring, persisting in time and maintaining rich ecosystems that may support populations of mammals being able to breathe and feed throughout the ice season (Ainley et al., 2010b; Arrigo and van Dijken, 2003; Karnovsky et al., 2007; Tremblay and Smith, 2007; Arrigo et al., 2015). Polynyas also support rich benthic communities through enhanced vertical carbon flux (Grebmeier and Barry, 2007). Sub-adult male SESs may also benefit from this by feeding on the shelf or slope regions without being constrained by sea ice. They likely feed on the most abundant pelagic finfish in Antarctic shelf water, the Antarctic silverfish (*Pleuragramma antarcticum)*, from surface to ~900m (Daneri and Carlini, 2002; La Mesa et al., 2010) or on epibenthic Antarctic toothfish (*Dissostichus mawsoni*) (Bradshaw et al., 2003; Smith et al., 2007) with juvenile finfish principally found on the shelf while adults are found along the slope (Ashford et al., 2012) sometimes shallower than though within ~1000 m of the water column (Watwood et al., 2006) or under fast ice in mid-depths (12–180 m; Fuiman et al. 2002). Shallow

ACCEPTED MANUSCRIPT

dives observed in high sea ice concentration close to the Antarctic coast (10 ± 6% of the total dives for males) could correspond to specific foraging activity associated with the rich under-ice community of fish and invertebrates (Ainley et al., 1991). Moreover, these dives were mostly performed at night, where the diurnal vertical migration of adult krill (*Euphausia crystallorophias*), more pronounced in winter than summer (Siegel 2012; Flores et al., 2012b; Cisewski and Strass 2016) might attract various preys, such as *Pleuragramma antarcticum* (Fuiman et al., 2002).

4.2 Seasonality in foraging activity

Our analysis highlights the importance of the seasonal cycle to the seal hunting time. For both males and females, we found that hunting time per dive increased from April to June. This is not surprising given that sea ice characteristics are intrinsically related to seasons, but whether the season itself (i.e. productivity of the ecosystem at a certain period) or seasonal changes in along-track sea ice habitat (i.e. access to favorable zones with prey availability later in the season) that affect seal foraging behaviour remains open to question.

When we considered the importance of $\mathcal{A}_{80\%}$ on the hunting time, we found that both males and females favored high values of $\mathcal{A}_{80\%}$. However, season was highly correlated with this variable. Is this result just reflecting that hunting time increases later on the season to fulfil ecological and/or physiological requirements or is it linked with changes in resources availability associated with high values of $\mathcal{A}_{80\%}$? In an attempt to answer this question, we considered the anomaly (from its seasonal cycle) of the sea ice cover around seal position ($\mathcal{A}'_{80\%}$). We found that years with positive values of $\mathcal{A}'_{80\%}$ were associated with shorter hunting times. We therefore speculate that the season is key to understand seal hunting time, with longest hunting time associated with autumn. And, within a given season, both males and females hunt longer when they were more patches of low concentrated sea ice around their position, which might provide to the animals easier access to air for breathing and therefore easier environment to hunt. Thus, to answer the previous question, increased hunting times were not linked with high values of $\mathcal{A}_{80\%}$.

We hypothesize that the time available to hunt may in fact decrease when the sea ice environment is constraining due to the fact that the animals have to add an horizontal component to the distance needed to reach prey. Thus, dive physiological limits may reduce the opportunity to hunt (where the seal slows down its vertical speed under a threshold of 0.4 $m.s^{-1}$). This is similar when prey is deeper, the seals have longer transit time to reach prey. The validity of hunting time is thus dependent on the sea ice constraint and diving depth, and above a certain depth (cf. Jouma'a et al., 2016) or a certain threshold of sea ice constraint, hunting time may be biased as shorter hunting times (reflecting the physiological dive limits) may be associated with good foraging success.

The under-ice ocean seasonal cycle is characterized by the presence of an autumn (May–June) bloom in sea ice (Fritsen et al., 1994; Lieser et al., 2015). Based on our previous hypothesis that the season itself affects foraging behaviour, we conclude that such an autumn bloom could affect hunting time through ecosystem cascades. Ice algal autumn blooms are generally not intense, but they are biologically significant and could provide a readily accessible food source for pelagic herbivores such as krill, which may in turn sustain upper trophic levels in autumn/early winter season (Meiners et al., 2012). Regarding polynyas, primary production in early spring/summer appears to extend feeding and reproduction in zooplankton (such as copepods and euphausiids) into late summer and early autumn (Deibel and Daly, 2007). Similarly, middle to upper trophic

ACCEPTED MANUSCRIPT

levels might benefit from this secondary production and concentrated resources through the autumn/early winter season.

Finally, buoyancy of the seal may also play a role in the positive correlation between hunting time and season. At the start of post-moult foraging trips, SESs are negatively buoyant, but along their trip, when they acquire resources and get fatter, they get closer to the neutral buoyancy (a critical factor of the swimming effort). It was found by Jouma'a et al. (2016) that the closer the seal was to neutral buoyancy the longer was the bottom duration, and consequently the hunting time.

4.3 Limits

The relationship between hunting time, foraging success and patch quality is complex and depends on several factors such as prey size, energy content, distribution and environmental conditions. However, for some questions, such as this research, where a species has a reasonably stable habitat use within each sex, relative changes in hunting time still provide very valuable insights. We made the choice to not discuss the fact that some of the "habitat preference" or value here associated with ice cover may be driven at least in part by bathymetry and depth of prey. We choose to develop discussion about prey types or resources associated with specific sea ice conditions. The goal of this study was not to determine the driving factor of seal foraging activity (which is from our point of view and from our past study Labrousse et al. (2015) a combination of bathymetric features, water masses properties and sea ice conditions) but to identify the influence of the spatio-temporal variability of sea ice on the seal foraging behaviour in terms of constraint and benefit. Considerable effort should be made to deploy accelerometers over the long winter trips of post-moult elephant seals. These new sensors enable the estimation of energy expenditure and intake. Finally, the time-series of descent vertical speed on low resolution dive data may be promising in describing the change in body condition.

5. Conclusion

Understanding the linkages between predators and sea ice is essential to any attempt to make robust and reliable predictions about ecosystem responses to future climate related sea ice change. For "non sea ice obligate species" such as SESs, the importance of sea ice patterns along their winter foraging trips are not well understood. It is known, however, that high-latitude marine ecosystems exploited by SESs are extensively influenced by the presence, seasonal rhythms and properties of sea ice (Massom and Stammerjohn, 2010). Here, we have confirmed important associations between seal foraging behaviour and sea ice, and we brought new insights on the role of the spatio-temporal variability of sea ice along their tracks. It builds upon previous studies that the responses of predators to sea ice and its variability are complex, involving aspects of seasonality and position within sea ice.

Our understanding of the complex linkages between sea ice and ecosystems still remains limited by restricted ship access, difficulties in sampling in remote environments during wintertime, and the patchiness of biota at any given location (Brierley & Thomas, 2002; Steffens et al., 2006). In addition, our understanding of the trophic ecology of benthic and mesopelagic communities that SESs consume within the sea ice region and their vertical distribution are extremely limited (Costa et al., 2010). Resource limitation due to low primary productivity in winter is often regarded as a key factor, however, we show in the present study that food

ACCEPTED MANUSCRIPT

consumption of the top predator community such as SESs persists or increases hundreds of kilometres deep into the pack ice (see also van Franeker et al., 1997; Flores et al., 2012b). Biological resources in ice-covered regions may have been underestimated by pelagic sampling in the past, and thus may appear poorer than they really are (Flores et al., 2012b). Moreover, the current neglect of an autumn bloom from non-detection of ice-associated phytoplankton in conventional satellite ocean-colour images may have also underestimate the potential of sea ice to sustain a rich under-ice ecosystem during winter (Lieser et al., 2015). Thus this work also contributes to deepening our knowledge on (i) the functioning of the under-ice biological habitat and (ii) ecological mechanisms that take place in remote and extreme environments with limited access.

The continued sustained monitoring of vertebrate colonies relative to sea ice parameters around the Antarctic coast and islands is crucial, given the complexity of the impact of climate forcing on biotic and abiotic components of the Antarctic marine ecosystem (Clarke et al., 2008; Massom and Stammerjohn, 2010).

Acknowledgements

This study is part of French Polar Institute (Institut Paul Emile Victor, IPEV) research project IPEV # 109, PI H. Weimerskirch, and of the Australian collaborative "Integrated Marine Observing System" (IMOS) research programme. It was funded by a CNES-TOSCA project ("Elephants de mer océanographes") and IMOS, and supported by the Australian Government through both the National Collaborative Research Infrastructure Strategy and the Super Science Initiative and the Cooperative Research Centre programme through the Antarctic Climate & Ecosystems Cooperative Research Centre. This work was also supported by the Japan Society for the Promotion of Science Grant-in-Aid for Scientific Research (KAKENHI) number 25.03748. J.B. Sallée received support from the ERC under the European Union's Horizon 2020 research and innovation program (grant agreement 637770). For R. Massom, A. Fraser and P. Reid, the work contributes to AAS Project 4116. MODIS data were obtained from the NASA Atmosphere Archive and Distribution System (http://ladsweb.nascom.nasa.gov). Passive microwave sea ice concentration data were obtained from the University of Bremen (http://www.iup.uni-bremen.de/seaice/amsr/) for AMSR-E, AMSR-2, and from the NASA Earth Observing System Distributed Active Archive Center (DAAC) at the U.S. National Snow and Ice Data Center, University of Colorado (http://www.nsidc.org) for SSMI/S. Special thanks go to J.O. Irisson, S. Bestley, S. Wotherspoon, M. Authier, B. Picard, A. Bosse, M. O'Toole and Y. David for very useful comments. Finally, we would like to thank N. El Skaby and all colleagues and volunteers involved in the research on southern elephant seals in Kerguelen. All animals in this study were treated in accordance with the IPEV ethical and Polar Environment Committees guidelines.

References

Ainley, D.G., Larue, M.A., Stirling, I., Stammerjohn, S., Siniff, D.B., 2015. An apparent population decrease, or change in distribution, of Weddell seals along the Victoria Land coast. Marine Mammal Science 31, 1338–1361. doi:10.1111/mms.12220.

Ainley, D., Russell, J., Jenouvrier, S., Woehler, E., Lyver, P.O., Fraser, W.R., Kooyman, G.L., 2010a. Antarctic penguin response to habitat change as Earth's troposphere reaches 2°C above preindustrial levels. Ecological Monographs 80, 49–66.

ACCEPTED MANUSCRIPT

Ainley, D.G., Fraser, W.R., Smith, W.O., Jr., Hopkins, T.L. and Torres, J.J., 1991. The structure of upper level pelagic food webs in the Antarctic: Effect of phytoplankton distribution. Journal of Marine Systems 2, 111-122.

Ainley, D. G., Fraser, W. R., Sullivan, C. W., Torres, J. J., Hopkins, T. L., & Smith, W. O., 1986. Antarctic mesopelagic micronekton: Evidence from seabirds that pack ice affects community structure. Science 232, 847-849

Ainley, D. G., Tynan, C. T. and Stirling, I., 2010b. Sea ice: A critical habitat for polar marine mammals and birds. In: Thomas, D. N. and Dieckmann, G. S. (Eds.), Sea ice 2. Blackwell Science, London, UK, 395–424.

Arrigo, K.R., van Dijken, G.L., 2003. Phytoplankton dynamics within 37 Antarctic coastal polynya systems. Journal of Geophysical Research 108. doi:10.1029/2002JC001739.

Arrigo, K.R., van Dijken, G.L., Strong, A., 2015. Environmental controls of marine productivity hot spots around Antarctica. Journal of Geophysical Research Oceans 120, 5545–5565. doi:10.1002/2015JC010888.

Ashford, J., Dinniman, M., Brooks, C., Andrews, A.H., Hofmann, E., Cailliet, G., Jones, C., Ramanna, N., Gillanders, B., 2012. Does large-scale ocean circulation structure life history connectivity in Antarctic toothfish (*Dissostichus mawsoni*)? Canadian Journal of Fisheries and Aquatic Sciences 69, 1903–1919. doi:10.1139/f2012-111.

Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432, 100–103. doi:10.1038/nature02996.

Bailleul, F., Authier, M., Ducatez, S., Roquet, F., Charrassin, J.-B., Cherel, Y., Guinet, C., 2010. Looking at the unseen: combining animal bio-logging and stable isotopes to reveal a shift in the ecological niche of a deep diving predator. Ecography 33, 709–719. doi:10.1111/j.1600-0587.2009.06034.x.

Bailleul, F., Charrassin, J.-B., Ezraty, R., Girard-Ardhuin, F., McMahon, C.R., Field, I.C., Guinet, C., 2007. Southern elephant seals from Kerguelen Islands confronted by Antarctic Sea ice. Changes in movements and in diving behaviour. Deep Sea Research Part II: Topical Studies in Oceanography 54, 343–355. doi:10.1016/j.dsr2.2006.11.005.

Banks, J., Lea, M.-A., Wall, S., McMahon, C.R., Hindell, M.A., 2014. Combining bio-logging and fatty acid signature analysis indicates spatio-temporal variation in the diet of the southern elephant seal, *Mirounga leonina*. Journal of Experimental Marine Biology and Ecology 450, 79–90. doi:10.1016/j.jembe.2013.10.024.

Barbraud, C., Rolland, V., Jenouvrier, S., Nevoux, M., Delord, K., Weimerskirch, H., 2012. Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a review. Marine Ecology Progress Series 454, 285–307. doi:10.3354/meps09616.

Barbraud, C., Weimerskirch, H., 2006. Antarctic birds breed later in response to climate change. Proceedings of the National Academy of Sciences 103, 6248–6251.

Barbraud, C., Weimerskirch, H., 2001. Emperor penguins and climate change. Nature 411, 183-186.

Bestley, S., Patterson, T. A., Hindell, M. A., and Gunn, J. S. 2010. Predicting feeding success in a migratory predator: integrating telemetry, environment, and modeling techniques. Ecology 91:2373–2384. http://dx.doi.org/10.1890/08-2019.1.

Biuw, M., Boehme, L., Guinet, C., Hindell, M., Costa, D., Charrassin, J.-B., Roquet, F., Bailleul, F., Meredith, M., Thorpe, S., 2007. Variations in behaviour and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. Proceedings of the National Academy of Sciences 104, 13705–13710.

Biuw, M., Nøst, O.A., Stien, A., Zhou, Q., Lydersen, C., Kovacs, K.M., 2010. Effects of hydrographic variability on the spatial, seasonal and diel diving patterns of southern elephant seals in the eastern Weddell Sea. PLoS ONE 5, e13816. doi:10.1371/journal.pone.0013816.

Bluhm, B.A., Gradinger, R.R., Schnack-Schiel, S.B., 2010. Sea ice meio- and macrofauna. In: Thomas, D. N. and Dieckmann, G. S. (Eds.), Sea ice 2. Blackwell Science, London, UK, 357–394.

Bornemann, H., Kreyscher, M., Ramdohr, S., Martin, T., Carlini, A., Sellmann, L., Plötz, J., 2000. Southern elephant seal movements and Antarctic sea ice. Antarctic Science 12, 3–15.

Bost, C.-A., Charrassin, J.-B., Clerquin, Y., Ropert-Coudert, Y., Le Maho, Y., others, 2004. Exploitation of distant marginal

ACCEPTED MANUSCRIPT

ice zones by king penguins during winter. Marine Ecology Progress Series 283, 293–297.

Bradshaw, C.J.A., Hindell, M.A., Best, N.J., Phillips, K.L., Wilson, G., Nichols, P.D., 2003. You are what you eat: describing the foraging ecology of southern elephant seals (*Mirounga leonina*) using blubber fatty acids. Proceedings of the Royal Society B: Biological Sciences 270, 1283–1292. doi:10.1098/rspb.2003.2371.

Brierley, A.N., Thomas, D.N., 2002. Ecology of Southern Ocean pack ice. Advances in Marine Biology 43, 171–276.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multi-model inference: a practical information-theoretic approach, Springer, New York, USA.

Chambert, T., Rotella, J. J. and Garrott, R. A., 2015. Female Weddell seals show flexible strategies of colony attendance related to varying environmental conditions. Ecology, 96, 479–488. doi:10.1890/14-0911.1.

Cherel, Y., Ducatez, S., Fontaine, C., Richard, P., Guinet, C., 2008. Stable isotopes reveal the trophic position and mesopelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. Marine Ecology Progress Series 370, 239–247. doi:10.3354/meps07673.

Cisewski, B., and Strass, V. H., 2016. Acoustic insights into the zooplankton dynamics of the eastern Weddell Sea. Progress in Oceanography, 144, 62-92.

Clarke, A., Brierley, A.S., Harris, C.M., Lubin, D., Smith, R.C., 2008. Polar and ice-edge marine systems, In: Polunin, N.V.C. (Ed.), Aquatic Ecosystems: Trends and Global Prospects. Cambridge University Press, Cambridge, UK, 319–333.

Constable, A.J., Melbourne-Thomas, J., Corney, S.P., Arrigo, K.R., Barbraud, C., Barnes, D.K.A., Bindoff, N.L., Boyd, P.W., Brandt, A., Costa, D.P., Davidson, A.T., Ducklow, H.W., Emmerson, L., Fukuchi, M., Gutt, J., Hindell, M.A., Hofmann, E.E., Hosie, G.W., Iida, T., Jacob, S., Johnston, N.M., Kawaguchi, S., Kokubun, N., Koubbi, P., Lea, M.-A., Makhado, A., Massom, R.A., Meiners, K., Meredith, M.P., Murphy, E.J., Nicol, S., Reid, K., Richerson, K., Riddle, M.J., Rintoul, S.R., Smith, W.O., Southwell, C., Stark, J.S., Sumner, M., Swadling, K.M., Takahashi, K.T., Trathan, P.N., Welsford, D.C., Weimerskirch, H., Westwood, K.J., Wienecke, B.C., Wolf-Gladrow, D., Wright, S.W., Xavier, J.C., Ziegler, P., 2014. Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. Global Change Biology 20, 3004–3025. doi:10.1111/gcb.12623.

Costa, D.P., Huckstadt, L.A., Crocker, D.E., McDonald, B.I., Goebel, M.E., Fedak, M.A., 2010. Approaches to Studying Climatic Change and its Role on the Habitat Selection of Antarctic Pinnipeds. Integrative and Comparative Biology 50, 1018–1030. doi:10.1093/icb/icq054.

Daneri, G., Carlini, A., 2002. Fish prey of southern elephant seals, *Mirounga leonina*, at King George Island. Polar Biology 25, 739–743.

David, C., Schaafsma, F.L., van Franeker, J.A., Lange, B., Brandt, A., Flores, H., 2016. Community structure of under-ice fauna in relation to winter sea-ice habitat properties from the Weddell Sea. Polar Biology. doi:10.1007/s00300-016-1948-4.

Deibel, D., Daly, K.L., 2007. Zooplankton Processes in Arctic and Antarctic Polynyas, In: Smith, W.O. and Barber, D.G. (Eds), Polynyas: Windows to the World. Elsevier Oceanography Series, Elsevier, 74, 271–322. http://dx.doi.org/10.1016/S0422-9894(06)74009-0.

Donnelly, J., Sutton, T.T., Torres, J.J., 2006. Distribution and abundance of micronekton and macrozooplankton in the NW Weddell Sea: relation to a spring ice-edge bloom. Polar Biology 29, 280–293. doi:10.1007/s00300-005-0051-z

Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernet, M., Fraser, W., 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. Philosophical Transactions of the Royal Society B: Biological Sciences 362, 67–94. doi:10.1098/rstb.2006.1955.

Eicken, H., 1992. The role of sea ice in structuring Antarctic ecosystems. Polar Biology 12, 3-13.

Flores, H., Van de Putte, A., Siegel, V., Pakhomov, E., van Franeker, J., Meesters, H., Volckaert, F., 2008. Distribution, abundance and ecological relevance of pelagic fishes in the Lazarev Sea, Southern Ocean. Marine Ecology

ACCEPTED MANUSCRIPT

Progress Series 367, 271–282. doi:10.3354/meps07530.

Flores, H., van Franeker, J.-A., Cisewski, B., Leach, H., Van de Putte, A.P., Meesters, E. (H.W.G.), Bathmann, U., Wolff, W.J., 2011. Macrofauna under sea ice and in the open surface layer of the Lazarev Sea, Southern Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 58, 1948–1961. doi:10.1016/j.dsr2.2011.01.010.

Flores, H., Atkinson, A., Kawaguchi, S., Krafft, B., Milinevsky, G., Nicol, S., Reiss, C., Tarling, G., Werner, R., Bravo Rebolledo, E., Cirelli, V., Cuzin-Roudy, J., Fielding, S., van Franeker, J., Groeneveld, J., Haraldsson, M., Lombana, A., Marschoff, E., Meyer, B., Pakhomov, E., Van de Putte, A., Rombolá, E., Schmidt, K., Siegel, V., Teschke, M., Tonkes, H., Toullec, J., Trathan, P., Tremblay, N., Werner, T., 2012a. Impact of climate change on Antarctic krill. Marine Ecology Progress Series 458, 1–19. doi:10.3354/meps09831.

Flores, H., van Franeker, J.A., Siegel, V., Haraldsson, M., Strass, V., Meesters, E.H., Bathmann, U., Wolff, W.J., 2012b. The association of Antarctic krill *Euphausia superba* with the under-ice habitat. PLoS ONE 7, e31775. doi:10.1371/journal.pone.0031775.

Forcada, J., Trathan, P.N., Boveng, P.L., Boyd, I.L., Burns, J.M., Costa, D.P., Fedak, M., Rogers, T.L., Southwell, C.J., 2012. Responses of Antarctic pack-ice seals to environmental change and increasing krill fishing. Biological Conservation 149, 40–50. doi:10.1016/j.biocon.2012.02.002.

Fraser, W.R., Hofmann, E.E., 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem. Marine Ecological Progress Series 265, 1–15.

Freckleton, R.P., 2011. Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. Behavioural Ecology and Sociobiology 65, 91–101. doi:10.1007/s00265-010-1045-6.

Fritsen, C.H., Lytle, V.I., Ackley, S.F., Sullivan, C.W., 1994. Autumn Bloom of Antarctic Pack-Ice Algae. Science 266, 782–784. doi:10.1126/science.266.5186.782.

Fuiman, L., Davis, R., Williams, T., 2002. Behaviour of midwater fishes under the Antarctic ice: observations by a predator. Marine Biology 140, 815–822. doi:10.1007/s00227-001-0752-y.

Grebmeier, J.M., Barry, J.P., 2007. Benthic Processes in Polynyas, In: Smith, W.O. and Barber, D.G. (Eds), Polynyas: Windows to the World. Elsevier Oceanography Series, Elsevier, 74, 363–390. http://dx.doi.org/10.1016/S0422-9894(06)74011-9.

Guinet, C., Cherel, Y., Ridoux, V., Jouventin, P., 1996. Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–85. Antarctic Science 8, 23–30.

Guinet, C., Vacquié-Garcia, J., Picard, B., Bessigneul, G., Lebras, Y., Dragon, A., Viviant, M., Arnould, J., Bailleul, F., 2014. Southern elephant seal foraging success in relation to temperature and light conditions: insight into prey distribution. Marine Ecology Progress Series 499, 285–301. doi:10.3354/meps10660.

Heerah, K., Hindell, M., Andrew-Goff, V., Field, I., McMahon, C.R., Charrassin, J.-B., 2017. Contrasting behavior between two populations of an ice-obligate predator in East Antarctica. Ecology and Evolution 7, 606–618. doi:10.1002/ece3.2652

Heerah, K., Hindell, M., Guinet, C., Charrassin, J.-B., 2015. From high-resolution to low-resolution dive datasets: a new index to quantify the foraging effort of marine predators. Animal Biotelemetry 3. doi:10.1186/s40317-015-0074-3.

Hindell, M.A., McMahon, C.R., Bester, M.N., Boehme, L., Costa, D., Fedak, M.A., Guinet, C., Herraiz-Borreguero, L., Harcourt, R.G., Huckstadt, L., Kovacs, K.M., Lydersen, C., McIntyre, T., Muelbert, M.M.C., Patterson, T., Roquet, F., Williams, G., Charrassin, J.B., 2016. Circumpolar habitat use in the southern elephant seal: implications for foraging success and population trajectories. Ecosphere 7.

Hindell, M.A., Bradshaw, C.J., Sumner, M.D., Michael, K.J., Burton, H.R., 2003. Dispersal of female southern elephant seals and their prey consumption during the austral summer: relevance to management and oceanographic zones. Journal of Applied Ecology 40, 703–715.

Hindell, M.A., Burton, H.R., Slip, D.J., 1991a. Foraging areas of southern elephant seals, *Mirounga leonina*, as inferred from water temperature data. Marine and Freshwater Research 42, 115–128.

ACCEPTED MANUSCRIPT

Hindell, M.A., Slip, D.J., Burton, H.R., 1991b. The Diving Behaviour of Adult Male and Female Southern Elephant Seals, *Mirounga Leonina* (Pinnipedia, Phocidae). Australian Journal of Zoology 39, 595–619.

Horning, M., Mellish, J., 2009. Spatially explicit detection of predation on individual pinnipeds from implanted post-mortem satellite data transmitters. Endangered Species Research 10, 135–143. doi:10.3354/esr00220.

Jenouvrier, S., Holland, M., Stroeve, J., Barbraud, C., Weimerskirch, H., Serreze, M., Caswell, H., 2012. Effects of climate change on an emperor penguin population: analysis of coupled demographic and climate models. Global Change Biology 18, 2756–2770. doi:10.1111/j.1365-2486.2012.02744.x.

Jouma'a, J., Le Bras, Y., Richard, G., Vacquié-Garcia, J., Picard, B., El Ksabi, N., Guinet, C., 2016. Adjustment of diving behaviour with prey encounters and body condition in a deep diving predator: the Southern Elephant Seal. Functional Ecology 30, 636–648. doi:10.1111/1365-2435.12514.

Karnovsky, N., Ainley, D.G., Lee, P., 2007. The Impact and Importance of Production in Polynyas to Top-Trophic Predators: Three Case Histories, In: Smith, W.O. and Barber, D.G. (Eds), Polynyas: Windows to the World. Elsevier Oceanography Series, Elsevier, 74, 391-410. http://dx.doi.org/10.1016/S0422-9894(06)74012-0.

Kaufmann, R.S., Smith Jr, K.L., Baldwin, R.J., Glatts, R.C., Robison, B.H., Reisenbichler, K.R., 1995. Effects of seasonal pack ice on the distribution of macrozooplankton and micronekton in the northwestern Weddell Sea. Marine Biology 124, 387–397.

Labrousse, S., Vacquié-Garcia, J., Heerah, K., Guinet, C., Sallée, J.-B., Authier, M., Picard, B., Roquet, F., Bailleul, F., Hindell, M., Charrassin, J.-B., 2015. Winter use of sea ice and ocean water mass habitat by southern elephant seals: The length and breadth of the mystery. Progress in Oceanography 137, 52–68. doi:10.1016/j.pocean.2015.05.023

Lancraft, T.M., Hopkins, T.L., Torres, J.J., Donnelly, J., 1991. Oceanic micronektonic/macrozooplanktonic community structure and feeding in ice covered Antarctic waters during the winter (AMERIEZ 1988). Polar Biology 11, 157–167.

Lancraft, T.M., Torres, J.J., and Hopkins, T.L., 1989. Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986). Polar Biology, 9, 225-233.

Lieser, J.L., Curran, M.A.J., Bowie, A.R., Davidson, A.T., Doust, S.J., Fraser, A.D., Galton-Fenzi, B.K., Massom, R.A., Meiners, K.M., Melbourne-Thomas, J., Reid, P.A., Strutton, P.G., Vance, T.R., Vancoppenolle, M., Westwood, K.J., Wright, S.W., 2015. Antarctic slush-ice algal accumulation not quantified through conventional satellite imagery: Beware the ice of March. The Cryosphere Discussions 9, 6187–6222. doi:10.5194/tcd-9-6187-2015, unpublished.

Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., Trivelpiece, S., 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic foodweb. Nature 387, 897–900.

Marschall, H.-P., 1988. The overwintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. Polar Biology 9, 129–135.

Massom, R.A., Stammerjohn, S.E., 2010. Antarctic sea ice change and variability – Physical and ecological implications. Polar Science 4, 149–186. doi:10.1016/j.polar.2010.05.001.

Massom, R.A., Stammerjohn, S.E., Smith, R.C., Pook, M.J., Iannuzzi, R.A., Adams, N., Martinson, D.G., Vernet, M., Fraser, W.R., Quetin, L.B., others, 2006. Extreme Anomalous Atmospheric Circulation in the West Antarctic Peninsula Region in Austral Spring and Summer 2001/02, and Its Profound Impact on Sea Ice and Biota*. Journal of climate 19, 3544–3571.

Massom, R., Hill, K., Barbraud, C., Adams, N., Ancel, A., Emmerson, L., Pook, M., 2009. Fast ice distribution in Adélie Land, East Antarctica: interannual variability and implications for emperor penguins *Aptenodytes forsteri*. Marine Ecology Progress Series 374, 243–257. doi:10.3354/meps07734.

Massom, R., Reid, P., Stammerjohn, S., Raymond, B., Fraser, A., Ushio, S., 2013. Change and variability in East Antarctic sea ice seasonality, 1979/80–2009/10. PLoS ONE 8, e64756. doi:10.1371/journal.pone.0064756.

McConnell, B.J., Chambers, C., Fedak, M.A., 1992. Foraging ecology of southern elephant seals in relation to the bathymetry

ACCEPTED MANUSCRIPT

and productivity of the Southern Ocean. Antarctic Science 4, 393–398.

McMahon, C.R., Bester, M.N., Burton, H.R., Hindell, M.A., Bradshaw, C.J., 2005. Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*. Mammal Review 35, 82–100.

Meiners, K.M., Vancoppenolle, M., Thanassekos, S., Dieckmann, G.S., Thomas, D.N., Tison, J.-L., Arrigo, K.R., Garrison, D.L., McMinn, A., Lannuzel, D., van der Merwe, P., Swadling, K.M., Smith, W.O., Melnikov, I., Raymond, B., 2012. Chlorophyll a in Antarctic sea ice from historical ice core data. Geophysical Research Letters 39, L21602. doi:10.1029/2012GL053478.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4, 133–142. doi:10.1111/j.2041-210x.2012.00261.x.

Nakagawa, S., Schielzeth, H., 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biological Reviews 85, 935-956. doi:10.1111/j.1469-185X.2010.00141.x.

Nicol, S., 2006. Krill, currents, and sea ice: *Euphausia superba* and its changing environment. Bioscience 56, 111–120.

Nicol, S., Pauly, T., Bindoff, N.L., Wright, S., 2000. Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. Science 260, 1617–1623.

Parkinson, C.L., Cavalieri, D.J., 2012. Antarctic sea ice variability and trends, 1979-2010. The Cryosphere 6, 871–880. doi:10.5194/tc-6-871-2012.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar D. and R Core Team, 2015. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-122, http://CRAN.R-project.org/package=nlme.

Pitman, R., 2011. Antarctic killer whales: top of the food chain at the bottom of the world. Journal of the American Cetacean Society 40, 39-45.

Proffitt, K.M., Garrott, R.A., Rotella, J.J., Siniff, D.B., Testa, J.W., 2007. Exploring linkages between abiotic oceanographic processes and a top-trophic predator in an Antarctic ecosystem. Ecosystems 10, 120–127. doi:10.1007/s10021-006-9003-x.

Raymond, B., Lea, M.-A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J.-B., Cottin, M., Emmerson, L., Gales, N., Gales, R., Goldsworthy, S.D., Harcourt, R., Kato, A., Kirkwood, R., Lawton, K., Ropert-Coudert, Y., Southwell, C., van den Hoff, J., Wienecke, B., Woehler, E.J., Wotherspoon, S., Hindell, M.A., 2015. Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. Ecography 38, 121–129. doi:10.1111/ecog.01021.

Siegel, V., 2012. Krill stocks in high latitudes of the Antarctic Lazarev Sea: seasonal and interannual variation in distribution, abundance and demography. Polar Biology 35, 1151–1177. doi:10.1007/s00300-012-1162-y.

Siniff, D.B., Garrott, R.A., Rotella, J.J., Fraser, W.R., Ainley, D.G., 2008. Opinion: Projecting the effects of environmental change on Antarctic seals. Antarctic Science 20, 425–435. doi:10.1017/S0954102008001351.

Smith, W.O., Ainley, D.G., Cattaneo-Vietti, R., 2007. Trophic interactions within the Ross Sea continental shelf ecosystem. Philosophical Transactions of the Royal Society B: Biological Sciences 362, 95–111. doi:10.1098/rstb.2006.1956.

Southwell, C., Emmerson, L., McKinlay, J., Newbery, K., Takahashi, A., Kato, A., Barbraud, C., DeLord, K., Weimerskirch, H., 2015. Spatially extensive standardized surveys reveal widespread, multi-decadal increase in East Antarctic Adélie penguin populations. PLOS ONE 10, e0139877. doi:10.1371/journal.pone.0139877.

Squire, V.A., 2007. Of ocean waves and sea-ice revisited. Cold Regions Science and Technology 49, 110–133. doi:10.1016/j.coldregions.2007.04.007.

Stammerjohn, S.E., Martinson, D.G., Smith, R.C., Yuan, X., Rind, D., 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern Annular Mode variability. Journal of Geophysical Research 113. doi:10.1029/2007JC004269.

Stammerjohn, S.E., Smith, R.C., 1997. Opposing Southern Ocean climate patterns as revealed by trends in regional sea ice coverage. Climatic Change 37, 617–639.

ACCEPTED MANUSCRIPT

Stammerjohn, S., Massom, R., Rind, D., Martinson, D., 2012. Regions of rapid sea ice change: An inter-hemispheric seasonal comparison:regions of rapid sea ice change. Geophysical Research Letters 39. doi:10.1029/2012GL050874.

Steffens, M., Piepenburg, D., Schmid, M.K., 2006. Distribution and structure of macrobenthic fauna in the eastern Laptev Sea in relation to environmental factors. Polar Biology 29, 837–848. doi:10.1007/s00300-006-0122-9.

Trathan, P.., Forcada, J., Murphy, E.., 2007. Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. Philosophical Transactions of the Royal Society B: Biological Sciences 362, 2351–2365. doi:10.1098/rstb.2006.1953.

Tremblay, J.-E., Smith, W.O., 2007. Primary Production and Nutrient Dynamics in Polynyas, In: Smith, W.O. and Barber, D.G. (Eds), Polynyas: Windows to the World. Elsevier Oceanography Series, Elsevier, 74, 239–269. http://dx.doi.org/10.1016/S0422-9894(06)74008-9.

Trivelpiece, W.Z., Hinke, J.T., Miller, A.K., Reiss, C.S., Trivelpiece, S.G., Watters, G.M., 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proceedings of the National Academy of Sciences 108, 7625–7628. doi:10.1073/pnas.1016560108.

van den Hoff, J., McMahon, C.R., Simpkins, G.R., Hindell, M.A., Alderman, R., Burton, H.R., 2014. Bottom-up regulation of a pole-ward migratory predator population. Proceedings of the Royal Society B: Biological Sciences 281, 20132842–20132842. doi:10.1098/rspb.2013.2842.

van Franeker, J.A., Bathmann, U.V., Mathot, S., 1997. Carbon fluxes to antarctic top predators. Deep Sea Research Part II: Topical Studies in Oceanography 44, 435–455. doi:10.1016/S0967-0645(96)00078-1.

Wadhams, P., 2000. Ice in the ocean. Gordon and Breach, Australia.

Walters, A., Lea, M.-A., van den Hoff, J., Field, I.C., Virtue, P., Sokolov, S., Pinkerton, M.H., Hindell, M.A., 2014. Spatially explicit estimates of prey consumption reveal a new krill predator in the Southern Ocean. PLoS ONE 9, e86452. doi:10.1371/journal.pone.0086452.

Watwood, S.L., Miller, P.J.O., Johnson, M., Madsen, P.T., Tyack, P.L., 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). Journal of Animal Ecology 75, 814–825. doi:10.1111/j.13652656.2006.01101.x.

Weimerskirch, H., Inchausti, P., Guinet, C., Barbraud, C., 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. Antarctic Science 15, 249–256. doi:10.1017/S0954102003001202.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems: Data exploration. Methods in Ecology and Evolution 1, 3–14. doi:10.1111/j.2041-210X.2009.00001.x.

Zuur, A.., Ieno, E.N., Walker, N.J., Saheliev, A.A., Smith, G.N., 2009. Mixed Effects Models and Extensions in Ecology With R. Springer, New York, USA.

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

Figures and Table

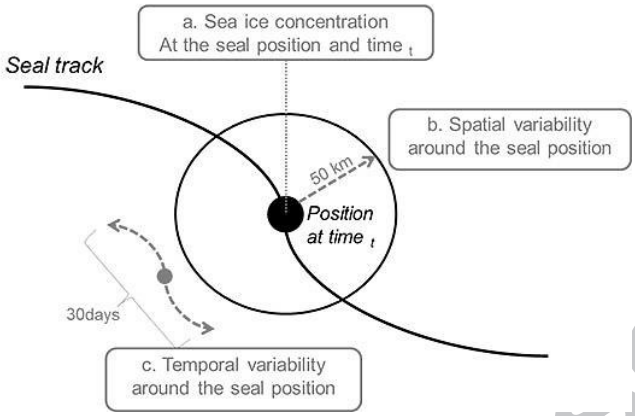


Fig 1. Schema illustrating the three sea ice variables used in the study: (a) the sea ice concentration at the position of the seal at the present time, (b) the area covered by sea ice with a concentration of >80% within a 50 km radius around the animal ($\mathcal{A}_{80\%}$) and (c) the number of days with a sea ice concentration of >80%at a given location within a 30 day window ($\mathcal{T}_{80\%}$).

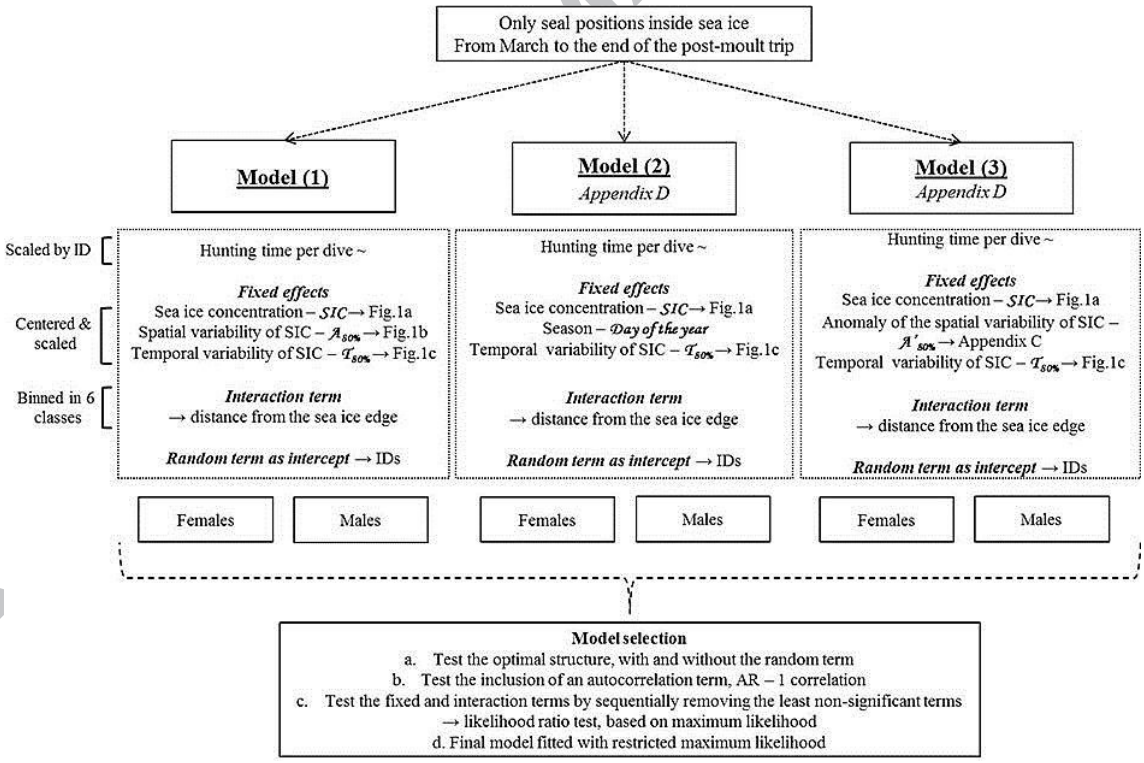


Fig 2. Schema illustrating the statistical approach step by step used for modelling the influence of sea ice parameters on foraging activity.

ACCEPTED MANUSCRIPT

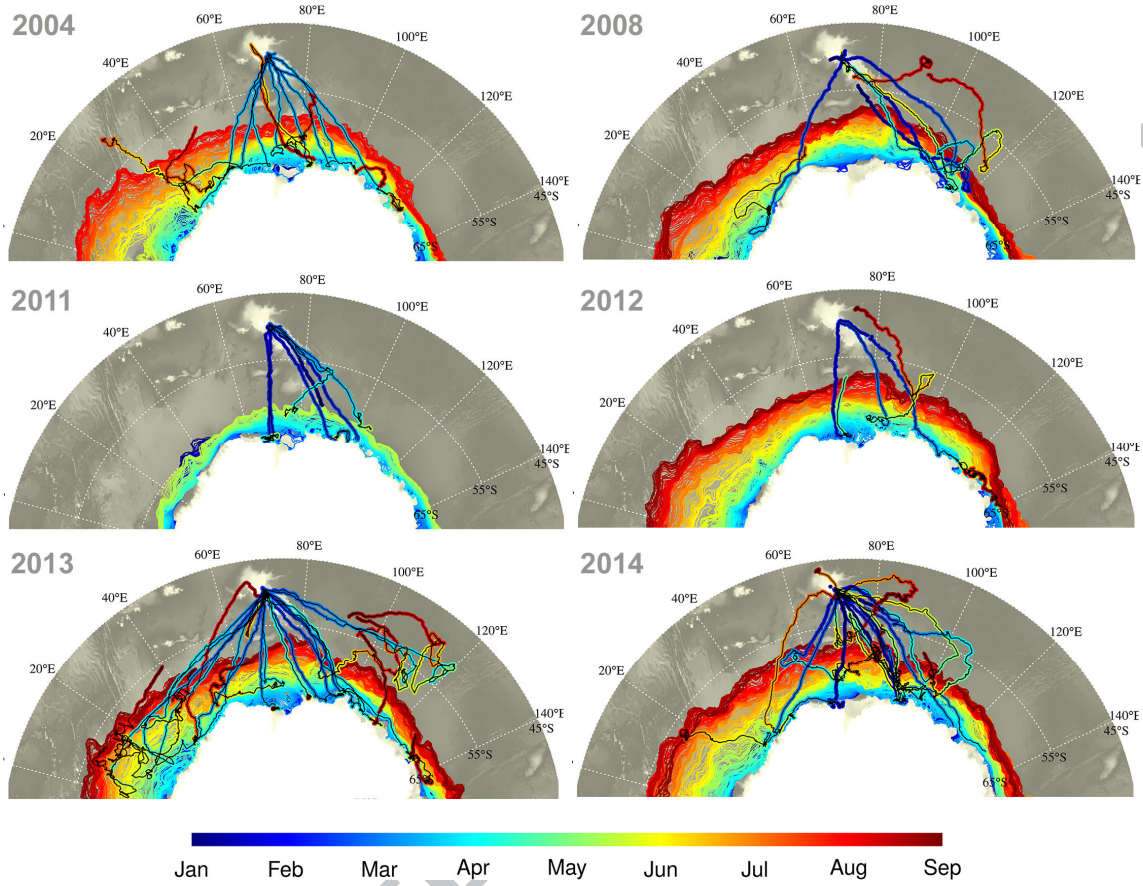


Fig 3. Tracks of the 46 post-moulting individuals equipped with CTD-SRDLs from 2004 to 2014, linked with the seasonality of the sea ice in the East Antarctic region. The colour scale represents the time and the same colour is used for sea ice extent and tracks of animals; the sea ice extent of a given day and associated seal positions are colored in the same way. For visual purposes, tracks and sea ice extent were limited to September (annual maximum sea ice extent) and the unique individual in 2009 was removed. For all years, sea ice extent was obtained from SSM/IS daily sea ice concentration (resolution 25 km).

ACCEPTED

ACCEPTED MANUSCRIPT

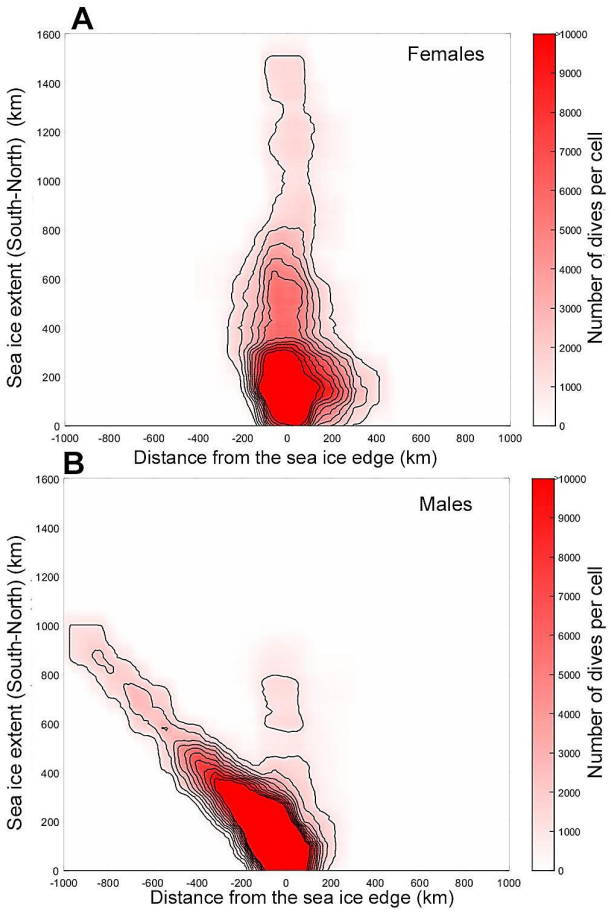


Fig 4. Density plots of the distance of females (A) and males (B) to the sea ice edge (km) relative to the increase of sea ice extent from South to North (km). Colour intensity represents the number of dives per grid cell of size 10 x 10 km (note that a sliding window over 200 x 200 km has been applied for smoothing purposes). Each contour represents 1000 dives. Negative distances on the x-axis indicate when seals are inside the sea ice region. Animal dives in the open ocean more than 200 km from the edge were not considered as they represent transit from/to the colony.

ACCEPTED MANUSCRIPT

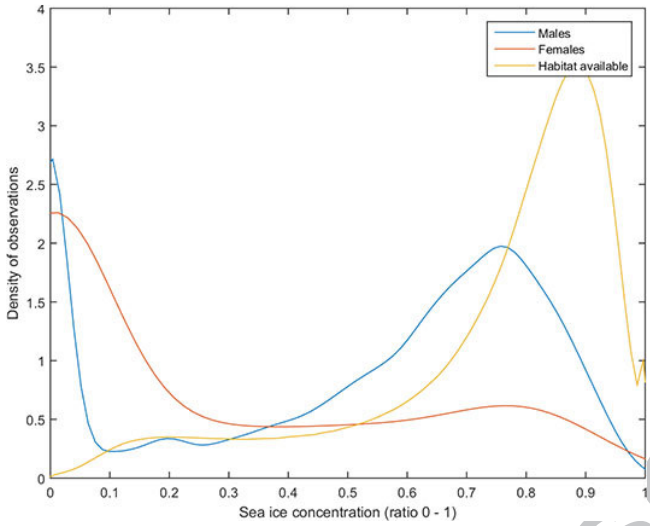


Fig 5. Density curves representing the habitat available to seals in the area of 0 - 150° E and from 55° S from March to September over the 7 years of the study in terms of sea ice concentration (yellow curve), and the sea ice usage by males (blue curve) and females (red curve). Observations north of 64°S with sea ice concentrations of < 15 % were removed. Sea ice concentration was obtained from SSM/IS daily sea ice concentration (resolution 25 km).

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

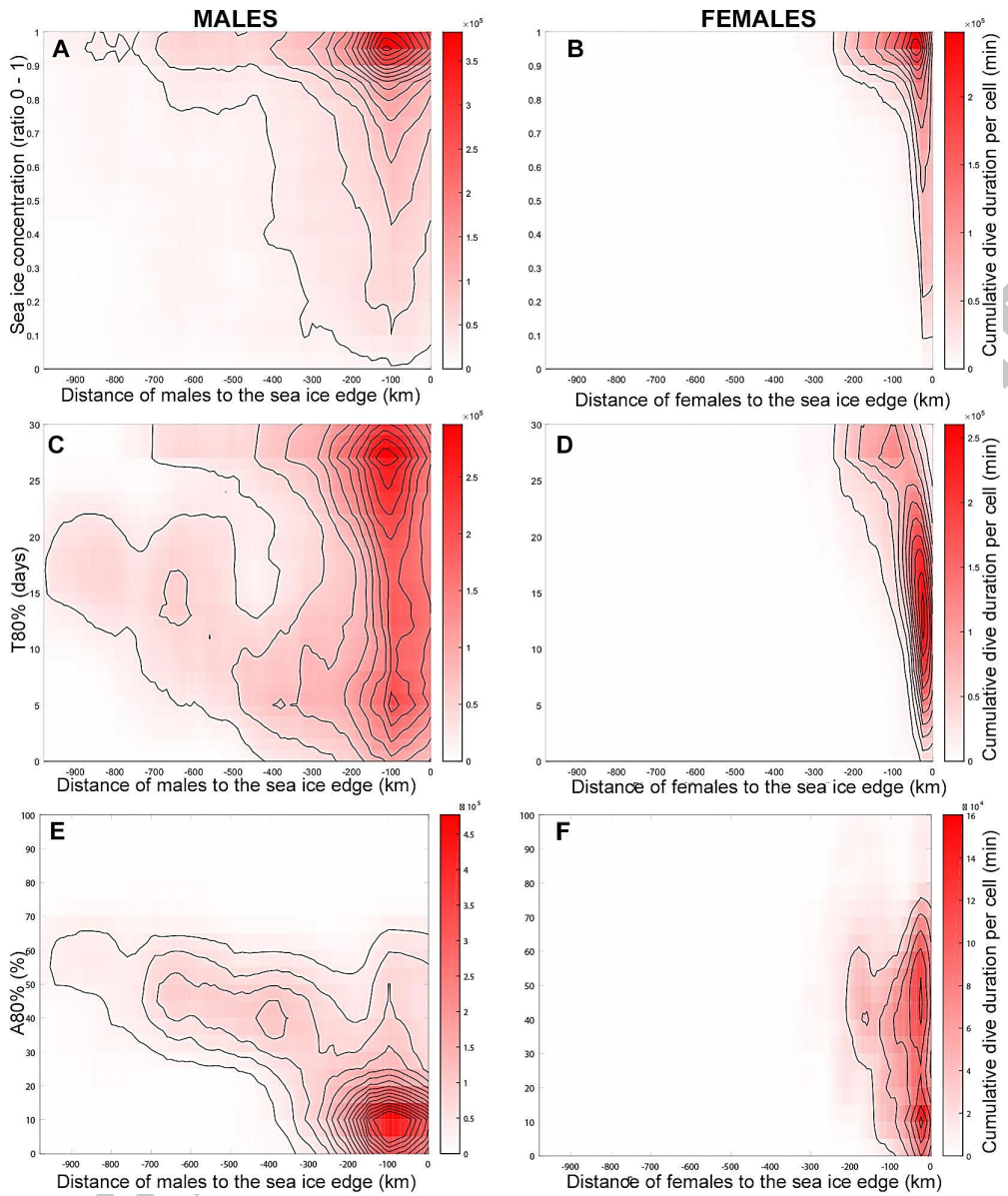


Fig 6. Density plot of the distance of males and females to the sea ice edge relative to: A, B) Sea ice concentration; C, D) The temporal variability of concentrated sea ice patches ($\mathcal{T}_{80\%}$, expressed as the number of days with sea ice concentration above 80% at a given location within a 30 day window); and E, F) The spatial variability of concentrated sea ice patches ($\mathcal{A}_{80\%}$, expressed by the area covered by sea ice with concentration above 80% within a 50 km radius around the animal). The colour scale represents the sum of dive duration (in minutes) per grid cell (note that a sliding window has been applied for smoothing purposes). Distances on the x-axis represent when seals are inside the sea ice zone, with values increasing towards the ice edge (at 0 km). One contour is drawn every $0.25.10^5$ min.

ACCEPTED MANUSCRIPT

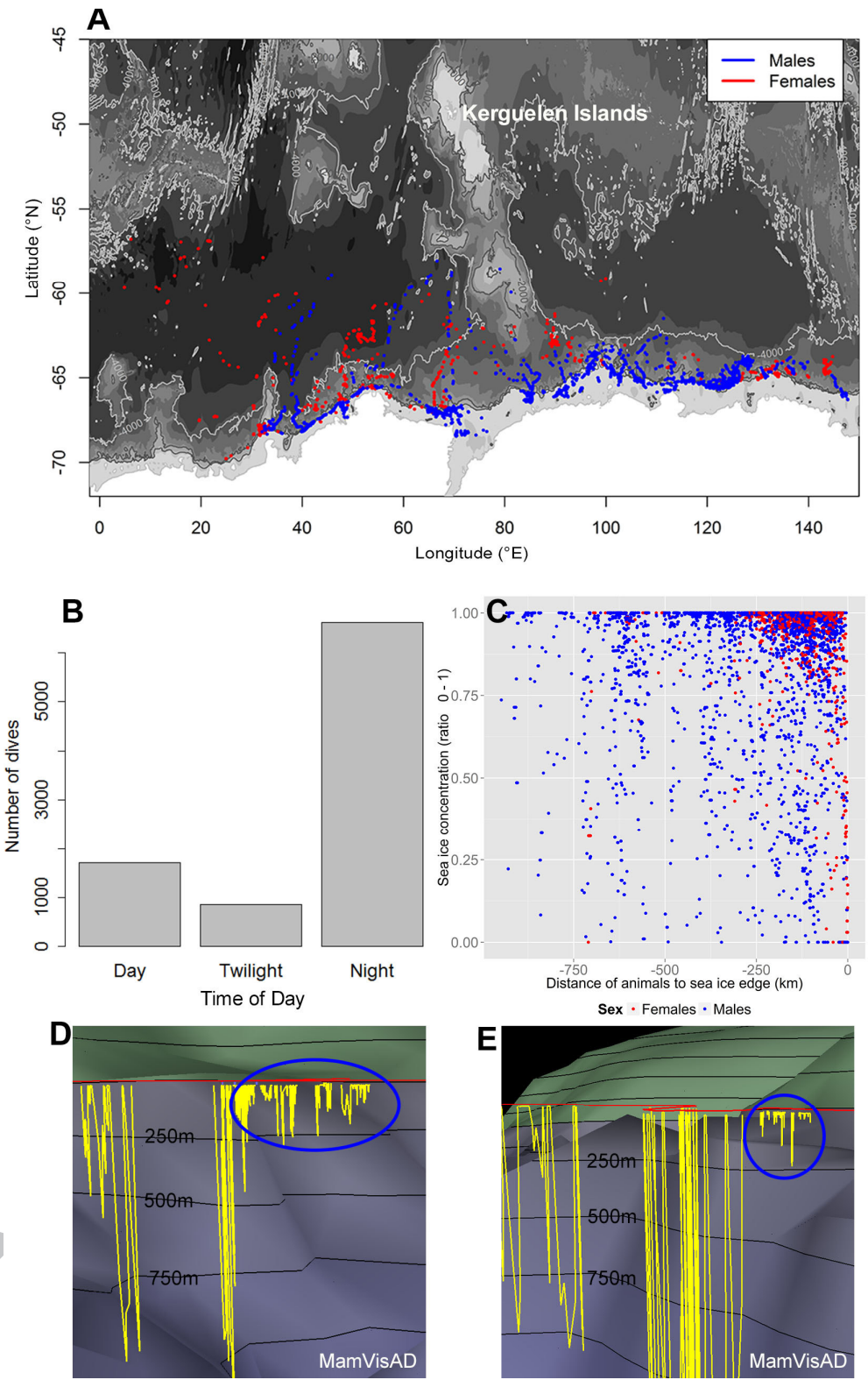


Fig 7. The characteristics of dives shallower than 40m for 22 males and 17 females equipped with CTD-SRDLs, from 2004 to 2014. A) Geographic repartition of shallow dives, with blue dots corresponding to male shallow dives and red dots to female shallow dives. The grey shading and contours correspond to bottom topography

ACCEPTED MANUSCRIPT

(m). B) A histogram of the frequency of shallow dives depending the time of day. C) Plot showing the relationship between sea ice concentration (ratio 0 - 1) and the distance of animals to the sea ice edge (in km) for the shallow dives. D-E) Examples of shallow dives for one male and one female, respectively, created with MamVisAD software (from the Sea Mammal Research Unit); dives are represented by yellow lines and red lines being the track of the seal. The blue ellipses show the presence of shallow dives.

ACCEPTED MANUSCRIPT

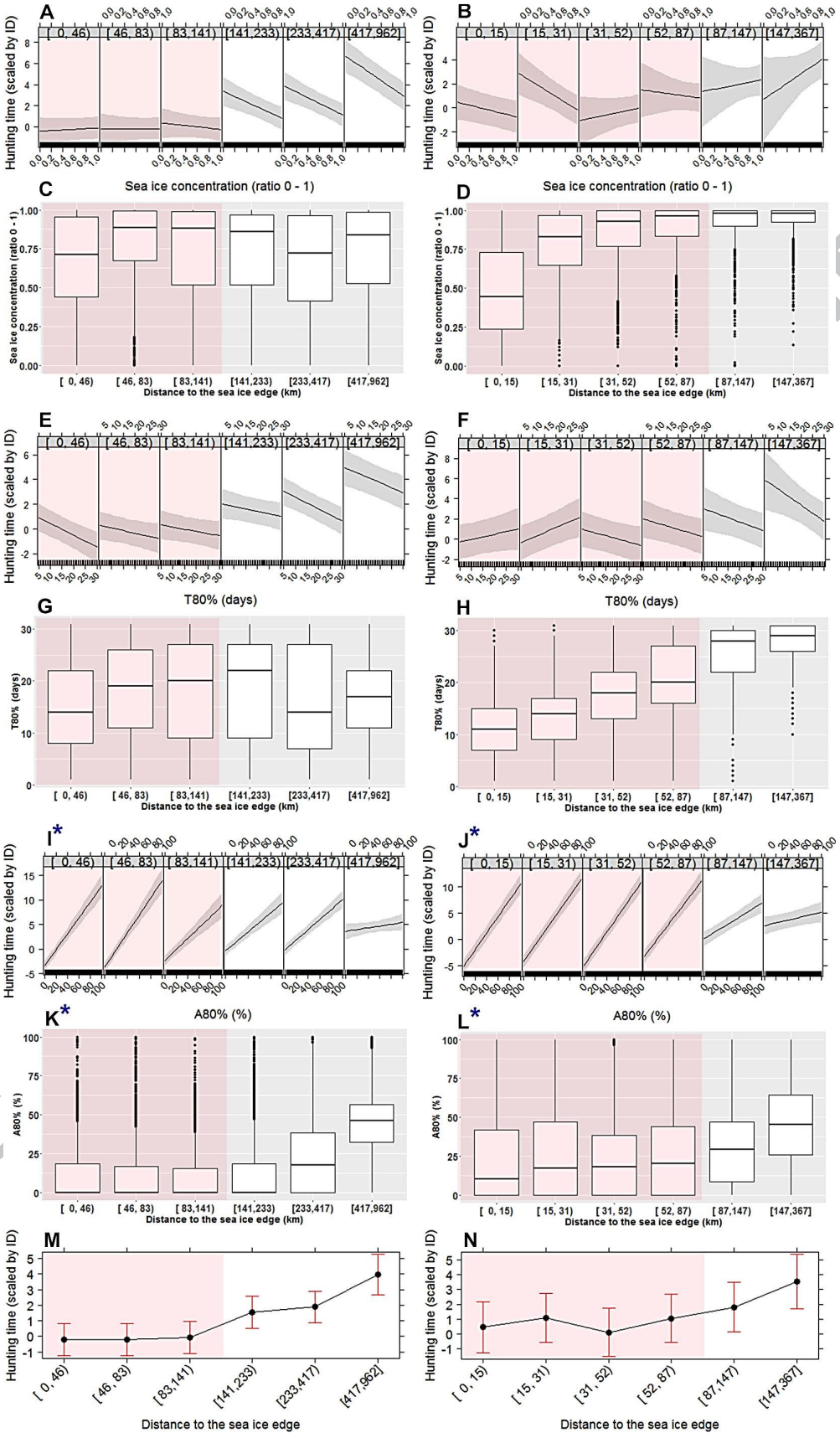
Table 1. Summary of regression coefficients and goodness-of-fit indices from the two most parsimonious models (LMMs) relating hunting time to sea ice patterns for the 19 females and 22 males equipped with CTD-SRDLs from 2004 to 2014. Coefficients are presented ± SE with their associated *p-value*. Significant parameters at the threshold 5% are denoted by bold characters. Six classes of distance of the animal from the sea ice edge were used in interaction with all the explanatory variables. Coefficients and *p-values* for the interaction between each explanatory variable and classes 2 – 6 were given relative to the class 1 of distance from the edge corresponding to 0-46 km for males and 0-15 km for females. Individuals were used as random effect on the intercept and explanatory variables were standardized to allow comparison of their slope coefficients.

ACCEPTED MANUSCRIPT

Linear mixed-effects model fit by REML : Response variable: Hunting time (scaled by ID)					
Males (n=22, dives=48787)			**Females (n=19, dives=36177)**		
Explanatory variables	**Coefficient ± SE**	**p-value**	**Explanatory variables**	**Coefficient ± SE**	**p-value**
Intercept has the baseline value of the class 1 of distance from the sea ice edge					
Intercept	-0.3 ± 0.5	0.5	**Intercept**	-0.5 ± 0.7	0.4
All parameters (for class 1 of distance from the sea ice edge)					
Sea ice concentration	0.1 ± 0.2	0.6	Sea ice concentration	**-0.3 ± 0.1**	**0.03***
Persitence of high SIC ($\mathcal{T}_{80\%}$)	**-0.9 ± 0.2**	**0*** **	Persitence of high SIC ($\mathcal{T}_{80\%}$)	0.6 ± 0.3	0.06
Area covered by high SIC ($\mathcal{A}_{80\%}$)	**3.2 ± 0.2**	**0*** **	Area covered by high SIC ($\mathcal{A}_{80\%}$)	**3.8 ± 0.2**	**0*** **
Bin of distance from the sea ice edge (relative to class 1)					
Class 2 [46, 83]	0.008 ± 0.3	0.9	Class 2 [15, 31]	**0.9 ± 0.4**	**0.03***
Class 3 [83,141]	0.2 ± 0.3	0.5	Class 3 [31, 52]	0.2 ± 0.4	0.6
Class 4 [141, 233]	**1.8 ± 0.3**	**0*** **	Class 4 [52, 87]	**1.5 ± 0.4**	**0*** **
Class 5 [233,417]	**2.1 ± 0.3**	**0*** **	Class 5 [87, 147]	**2.7 ± 0.5**	**0*** **
Class 6 [417,962]	**4.3 ± 0.5**	**0*** **	Class 6 [147, 367]	**3.9 ± 0.6**	**0*** **
Sea ice concentration (relative to class 1 of distance from the sea ice edge)					
SIC:Class 2 [46, 83]	-0.08± 0.3	0.8	SIC:Class 2 [15, 31]	-0.5 ± 0.2	0.06
SIC:Class 3 [83,141]	-0.3 ± 0.3	0.3	SIC:Class 3 [31, 52]	**0.6 ± 0.3**	**0.04***
SIC:Class 4 [141, 233]	**-0.9 ± 0.3**	**0.002****	SIC:Class 4 [52, 87]	0.1 ± 0.3	0.7
SIC:Class 5 [233,417]	**-0.9 ± 0.3**	**0*** **	SIC:Class 5 [87, 147]	0.6 ± 0.5	0.2
SIC:Class 6 [417,962]	**-1.3 ± 0.3**	**0*** **	SIC:Class 6 [147, 367]	**1.2 ± 0.5**	**0.02****
Persitence of high SIC, $\mathcal{T}_{80\%}$ (relative to class 1 of distance from the sea ice edge)					
$\mathcal{T}_{80\%}$:Class 2 [46, 83]	0.5 ± 0.3	0.08	$\mathcal{T}_{80\%}$:Class 2 [15, 31]	0.2 ± 0.4	0.6
$\mathcal{T}_{80\%}$:Class 3 [83,141]	0.6 ± 0.3	0.053	$\mathcal{T}_{80\%}$:Class 3 [31, 52]	**-1 ± 0.4**	**0.01***
$\mathcal{T}_{80\%}$:Class 4 [141, 233]	0.5 ± 0.3	0.09	$\mathcal{T}_{80\%}$:Class 4 [52, 87]	**-1 ± 0.4**	**0.02***
$\mathcal{T}_{80\%}$:Class 5 [233,417]	0.002 ± 0.3	0.9	$\mathcal{T}_{80\%}$:Class 5 [87, 147]	**-1 ± 0.5**	**0.03***
$\mathcal{T}_{80\%}$:Class 6 [417,962]	0.1 ± 0.3	0.6	$\mathcal{T}_{80\%}$:Class 6 [147, 367]	-1.1 ± 0.6	0.07
Area covered by high SIC, $\mathcal{A}_{80\%}$ (relative to class 1 of distance from the sea ice edge)					
$\mathcal{A}_{80\%}$:Class 2 [46, 83]	0.3 ± 0.3	0.3	$\mathcal{A}_{80\%}$:Class 2 [15, 31]	-0.05 ± 0.2	0.8
$\mathcal{A}_{80\%}$:Class 3 [83,141]	**-1 ± 0.3**	**0*** **	$\mathcal{A}_{80\%}$:Class 3 [31, 52]	0.01 ± 0.3	0.9
$\mathcal{A}_{80\%}$:Class 4 [141, 233]	**-1.3 ± 0.3**	**0****	$\mathcal{A}_{80\%}$:Class 4 [52, 87]	-0.3 ± 0.3	0.3
$\mathcal{A}_{80\%}$:Class 5 [233,417]	**-1.2 ± 0.3**	**0*** **	$\mathcal{A}_{80\%}$:Class 5 [87, 147]	**-2.2 ± 0.3**	**0*** **
$\mathcal{A}_{80\%}$:Class 6 [417,962]	**-2.9 ± 0.4**	**0*** **	$\mathcal{A}_{80\%}$:Class 6 [147, 367]	**-3.2 ± 0.3**	**0*** **
Goodness-of-fit					
$R^2_{LMM(m)\text{-}full}$	**14%**		$R^2_{LMM(m)\text{-}full}$	**13%**	
$R^2_{LMM(c)\text{-}full}$	**21%**		$R^2_{LMM(c)\text{-}full}$	**18%**	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*'.

ACCEPTED MANUSCRIPT



ACCEPTED MANUSCRIPT

Fig 8. Model 1, relationships from the two LMMs between hunting time and: A, B) the sea ice concentration at the seal position; E, F) the temporal variability of concentrated sea ice patches ($\mathcal{T}_{80\%}$); I, J) the spatial variability of concentrated sea ice patches ($\mathcal{A}_{80\%}$); and M, N) the distance of animals from the sea ice edge. Results for males are presented on the left panels and those for females on the right. Each graph from models shows the relationship relative to bin of the distance of the animal from the sea ice edge when inside the sea ice region (in km). For each graph, the thick lines represent the predictive values from the population at a given position in sea ice and the grey shaded envelopes represent the boundaries of the variation between the predicted values per individual. Available data for each bin of distance are represented by boxplots for: C, D) sea ice concentration; G, H) the temporal variability of concentrated sea ice patches ($\mathcal{T}_{80\%}$); and K, L) the spatial variability of concentrated sea ice patches ($\mathcal{A}_{80\%}$). The marginal ice zone is shown by the red shaded area. The variable differing between the three model suites was represented by blue stars (see Appendix D, Fig D1-D2).

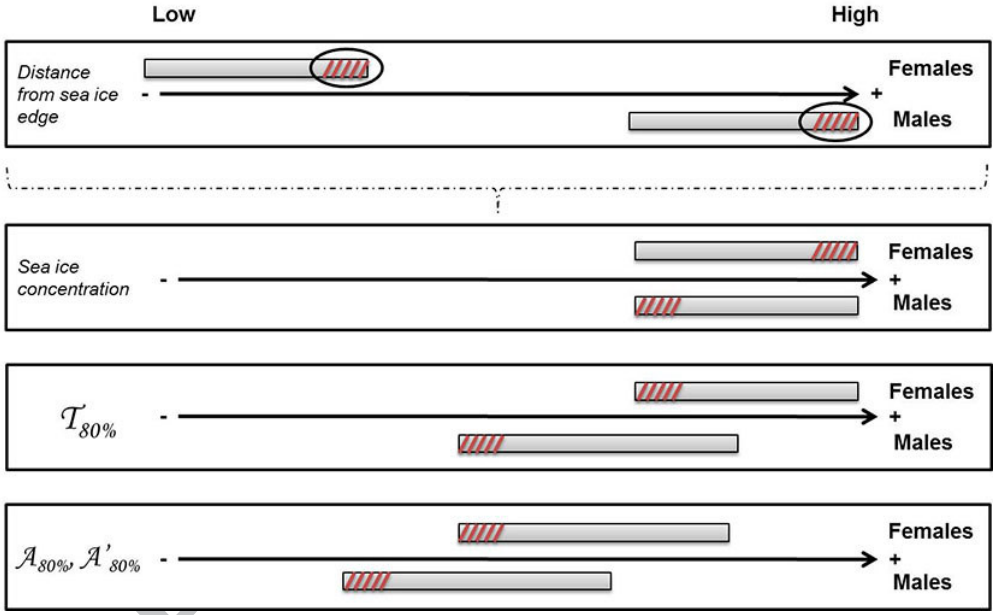


Fig 9. Summary schematic of the model analysis. Results for sea ice concentration, the temporal variability of concentrated sea ice patches ($\mathcal{T}_{80\%}$) and the spatial variability of concentrated sea ice patches ($\mathcal{A}_{80\%}$) are presented for sectors where males and females foraged more intensively, i.e. 150 - 370 km from the edge for females and 420 – 960 km from the edge for males. Grey bars represent their habitat use in these sectors, while red hatched lines represent where they foraged more intensively.

ACCEPTED MANUSCRIPT

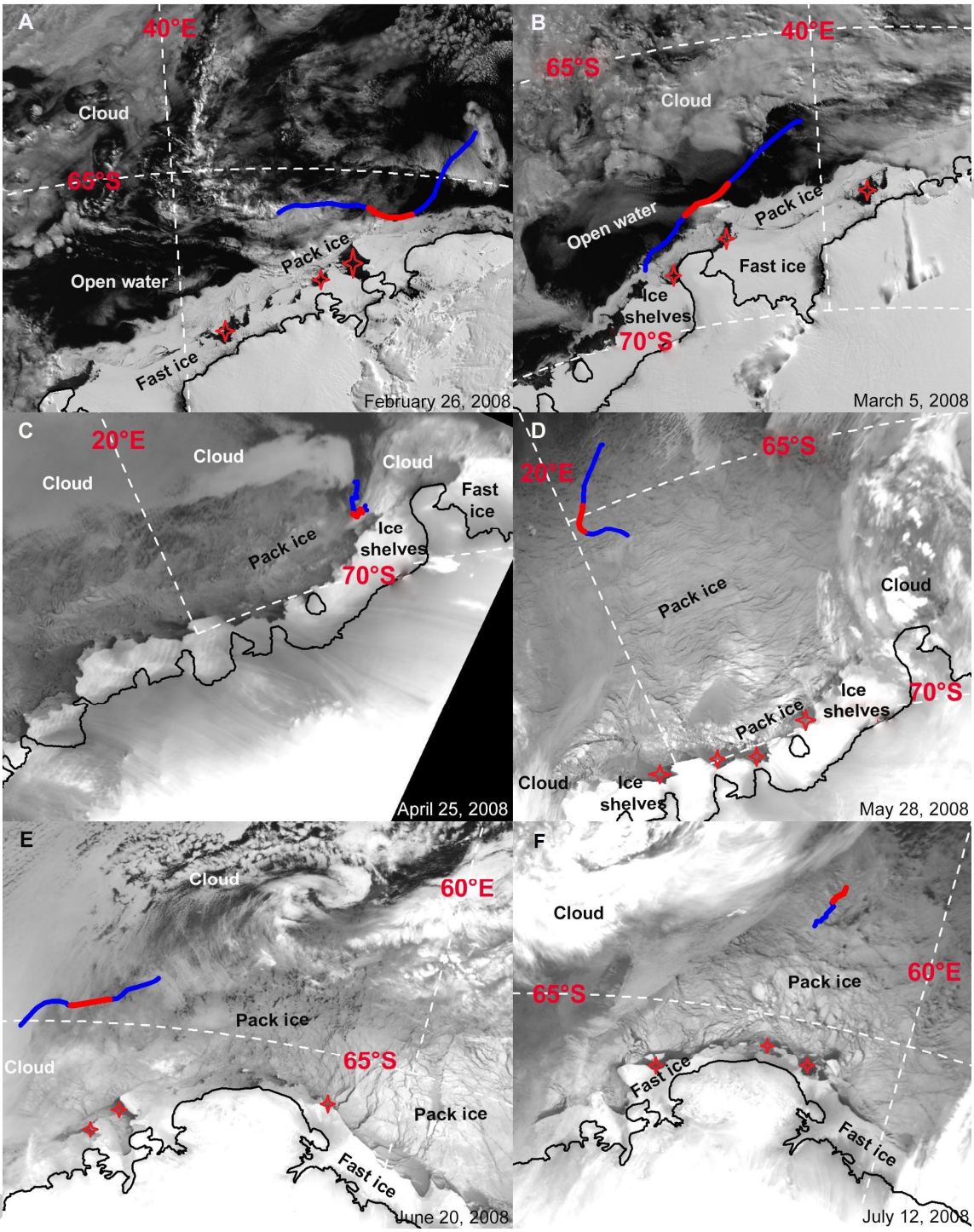
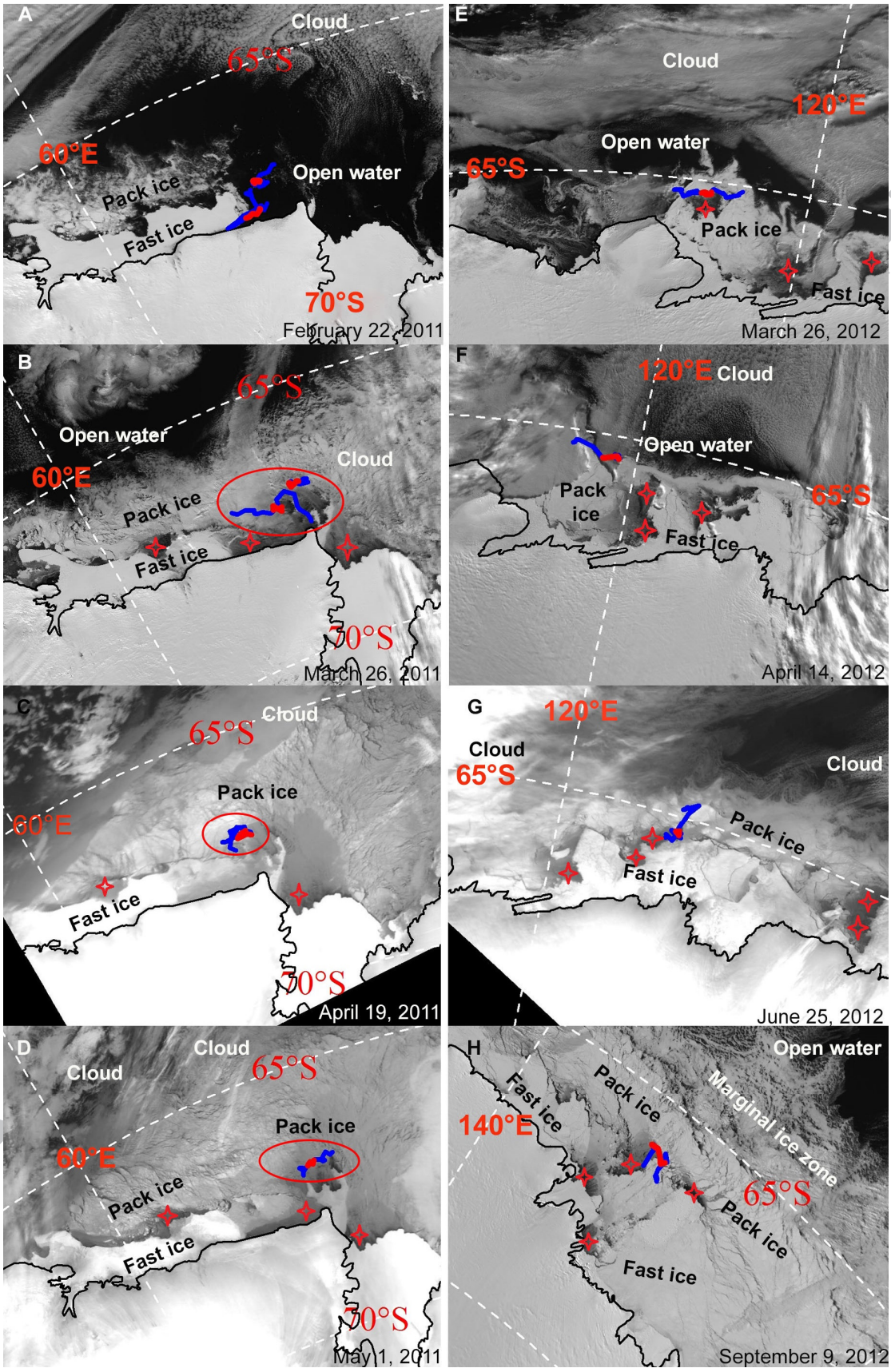


Fig 10. Time-series of MODIS visible and infrared images of resolution 1 km illustrating female behaviour within sea ice from February to July 2008 within the region from 20 to 50°E. Coincident day animal track is represented by a red curve, while the blue part corresponds to the previous and subsequent two days. Polynyas and large open water areas are represented by red stars.

ACCEPTED MANUSCRIPT



ACCEPTED MANUSCRIPT

Fig 11. Time-series of MODIS visible images of resolution 1 km illustrating male behaviour within sea ice from February to May 2011 within the region from 60 to 80°E (A-D) and from March to September 2012 within the region from 110 to 150°E (E-H). Coincident day animal track is represented by a red curve, while the blue part corresponds to the previous and subsequent two days. Polynyas and large open water areas are represented by red stars while red ellipses show where animals are within the Cape Darnley polynya.

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

Appendix A

Table 1. General information of the 46 post-moulting SES including sex, dive start and end date, date of return when the tag did not stopped, number of Argos position transmitted daily, animal weight and snout-to-tail length upon deployment, total number of dives, mean number of dives per day and mean distance travelled per day between the first and last locations of each day. Additional information on behaviour towards sea ice is also included such as animals visiting the sea ice region, their maximal distance from the sea ice edge, the percentage of shallow dives (i.e. less or equal to 40m) performed under sea ice and their hunting time per dive. Negative distances refer to distances into the pack from the ice edge, and positive distances refer to distances north of the ice edge. Mean are expressed ± SD.

ID	Sex	Dive start date	Dive end date	Date of return to the colony (if tag did not stopped)	Number of position transmitted daily	Weight (kg)	Length (cm)	Total dives	Daily number of dives	Distance travelled per day (km)	Visit sea ice	Maximal distance from the sea ice edge (km)	Shallow dives within sea ice (%)	Hunting time per dive within sea ice (min)
2004_1	M	04/03/2004	29/03/2004		8 ± 4	368	250	553	25 ± 12	75 ± 49	×	-62	12%	5,4 ± 3,9
2004_2	M	27/02/2004	09/07/2004		18 ± 7	385,5	267	6133	46 ± 20	34 ± 33	×	-192	7%	11,3 ± 7,3
2004_3	F	01/03/2004	19/07/2004		14 ± 9	297,5	233	5363	38 ± 20	34 ± 29	×	-345	1%	14,6 ± 11,3
2004_5	M	25/02/2004	06/08/2004		17 ± 6	469,5	282	7209	46 ± 18	22 ± 31	×	-341	10%	14 ± 10
2004_6	F	22/02/2004	07/08/2004		12 ± 6	347	240	4248	27 ± 12	28 ± 26	×	-165	1%	22 ± 10,2
2004_7	F	29/02/2004	02/08/2004		15 ± 9	295,5	238	6021	40 ± 19	42 ± 28	×	-110	2%	8,5 ± 4
2004_8	M	27/02/2004	08/08/2004	6 then South	17 ± 9	274	235	7530	50 ± 25	40 ± 34	×	-610	6%	5,4 ± 4,7
2004_10	F	29/02/2004	08/08/2004		16 ± 10	363,5	258	7503	46 ± 24	31 ± 29	×	-367	5%	13 ± 10
2008_1	M	01/01/2008	08/09/2008		9 ± 5	266	230	8815	39 ± 30	33 ± 26	×	-161	8%	10 ± 7,5
2008_2	F	24/12/2007	27/05/2008		14 ± 7	169	200	6031	39 ± 16	44 ± 30		-8		
2008_6	F	24/01/2008	16/08/2008		11 ± 4	290	242	6200	31 ± 10	42 ± 26	×	-3	0%	11,3 ± 6,2
2008_7	F	27/01/2008	11/07/2008		15 ± 7	377	267	5253	32 ± 13	44 ± 32	×	-244	1%	17 ± 9,8
2009_16	M	01/01/2009	03/06/2009	6	17 ± 7	258	249	5887	40 ± 18	34 ± 28	×	-155	4%	9,4 ± 7
2011_1	M	27/01/2011	20/02/2011		21 ± 7	680	316	1002	40 ± 13	98 ± 30		50		
2011_4	M	31/01/2011	16/05/2011		26 ± 7	800	330	4438	42 ± 11	33 ± 39	×	-316	2%	13,5 ± 7,1
2011_6	F	19/02/2011	16/05/2011		31 ± 9	284,6	233	4230	50 ± 11	32 ± 31	×	-4	0%	10,6 ± 5,8
2011_7	M	26/01/2011	15/04/2011		34 ± 10	452,5	280	4749	60 ± 19	36 ± 39	×	-302	14%	9,3 ± 6,5
2011_9	M	27/01/2011	16/05/2011		18 ± 6	628,5	326	3487	32 ± 12	29 ± 37	×	-409	7%	14,6 ± 9
2011_10	F	24/02/2011	16/05/2011		20 ± 9	330	250	3041	37 ± 11	35 ± 28	×	-37	0%	14,5 ± 8
2012_1	M	23/01/2012	14/09/2012		18 ± 6	523	291	9799	43 ± 18	31 ± 28	×	-434	19%	10,6 ± 11,1
2012_3	M	23/01/2012	26/04/2012		24 ± 6	454	277	4297	45 ± 11	36 ± 38	×	-286	1%	13,2 ± 6,2
2012_2	F	07/02/2012	28/09/2012	9	20 ± 9	303	233	7178	31 ± 12	28 ± 21	×	-58	1%	17 ± 9,1

ACCEPTED MANUSCRIPT

2013_1	F	27/02/2013	19/10/2013	10	18 ± 6	340	262	8079	34 ± 9	43 ± 30	×	-130	2%	17,5 ± 10,4
2013_2	M	08/03/2013	02/11/2013	11	17 ± 10	1100	370	8321	39 ± 17	33 ± 41	×	-482	6%	17,4 ± 10,5
2013_3	M	10/02/2013	17/03/2013		22 ± 9	468	280	1513	46 ± 9	67 ± 41	×	-140	19%	7,2 ± 5,7
2013_4	M	03/03/2013	09/09/2013	9	18 ± 7	850	333	6064	35 ± 12	36 ± 36	×	-699	9%	18,1 ± 11,5
2013_5	F	24/02/2013	17/12/2013	9 then South	22 ± 8	336	254	11732	43 ± 16	29 ± 27	×	-745	8%	16 ± 11,9
2013_7	F	17/02/2013	13/10/2013		19 ± 7	410	248	9204	42 ± 14	43 ± 36	×	-256	9%	15,1 ± 10,7
2013_9	M	11/02/2013	14/03/2013		24 ± 6	470	300	1517	47 ± 15	63 ± 45	×	-157	9%	9,1 ± 5,8
2013_11	M	11/02/2013	08/10/2013		23 ± 7	556	256	10151	44 ± 13	22 ± 32	×	-962	9%	12 ± 8,1
2013_12	M	17/02/2013	07/10/2013	10	19 ± 7	1150	375	7728	36 ± 12	31 ± 21	×	-164	5%	23,3 ± 10
2013_13	M	10/02/2013	20/04/2013		23 ± 6	600	321	3501	50 ± 17	50 ± 37	×	-221	18%	6,8 ± 6
2013_14	M	17/03/2013	24/11/2013	11	20 ± 8	300	270	10074	42 ± 16	19 ± 32	×	-743	19%	15 ± 11,2
2013_15	F	10/02/2013	29/09/2013	10	20 ± 7	366	248	8335	38 ± 9	47 ± 26	×	-121	2%	17,8 ± 10,3
2013_18	F	07/02/2013	03/08/2013		23 ± 9	346	255	6723	41 ± 15	34 ± 30	×	-192	1%	21,6 ± 8,5
2014_1	F	28/01/2014	21/09/2014	6 then East	17 ± 6	265	250	7760	35 ± 9	38 ± 25		136		±
2014_2	F	25/01/2014	30/03/2014		24 ± 10	304	255	2793	48 ± 15	56 ± 31	×	-34	20%	8,3 ± 6,3
2014_3	F	25/01/2014	04/10/2014	10	16 ± 6	293	244	7038	29 ± 8	28 ± 21	×	-64	0%	28 ± 10,1
2014_4	F	30/01/2014	12/03/2014		22 ± 9	265	236	1840	45 ± 13	57 ± 32		31		
2014_5	F	27/01/2014	23/09/2014		18 ± 4	244	240	7836	37 ± 8	23 ± 18		256		
2014_6	F	28/01/2014	30/09/2014	9	19 ± 6	266	243	8241	36 ± 10	32 ± 23	×	-128	1%	22,7 ± 9,2
2014_7	M	26/12/2013	23/10/2014	7 then South	19 ± 9	405	277	11722	46 ± 21	32 ± 32	×	-857	20%	9,1 ± 8,3
2014_8	F	30/01/2014	21/09/2014		17 ± 6	270	247	7249	34 ± 10	28 ± 25	×	-203	3%	21,2 ± 10,1
2014_9	M	29/12/2013	11/09/2014		12 ± 6	700	322	4233	22 ± 10	35 ± 32	×	-195	3%	23,5 ± 11,1
2014_10	M	27/12/2013	27/09/2014	6 then North	14 ± 8	700	306	7876	35 ± 14	27 ± 36	×	-241	12%	14,5 ± 8,7
2014_11	F	29/01/2014	17/09/2014		24 ± 13	295	249	8346	38 ± 19	28 ± 26	×	-148	9%	14,7 ± 9,2
Mean ± SD	_	_	_		18 ± 9	_	_	_	39 ± 17	34 ± 31	_		12%	14 ± 11
Sum	_	_	_		_	_	_	286843	_	_	_			
Mean ± SD males	_	_	_		_	559 ± 244	293 ± 39	_	41 ± 19	32 ± 35	_	-337 ± 267 (min males = -962)	10 ± 6 %	13 ± 10
Mean ± SD females	_	_	_		_	307 ± 52	245 ± 13	_	37 ± 14	35 ± 28	_	-128 ± 195 (min females = -745)	4 % ± 5%	17 ± 11

ACCEPTED MANUSCRIPT

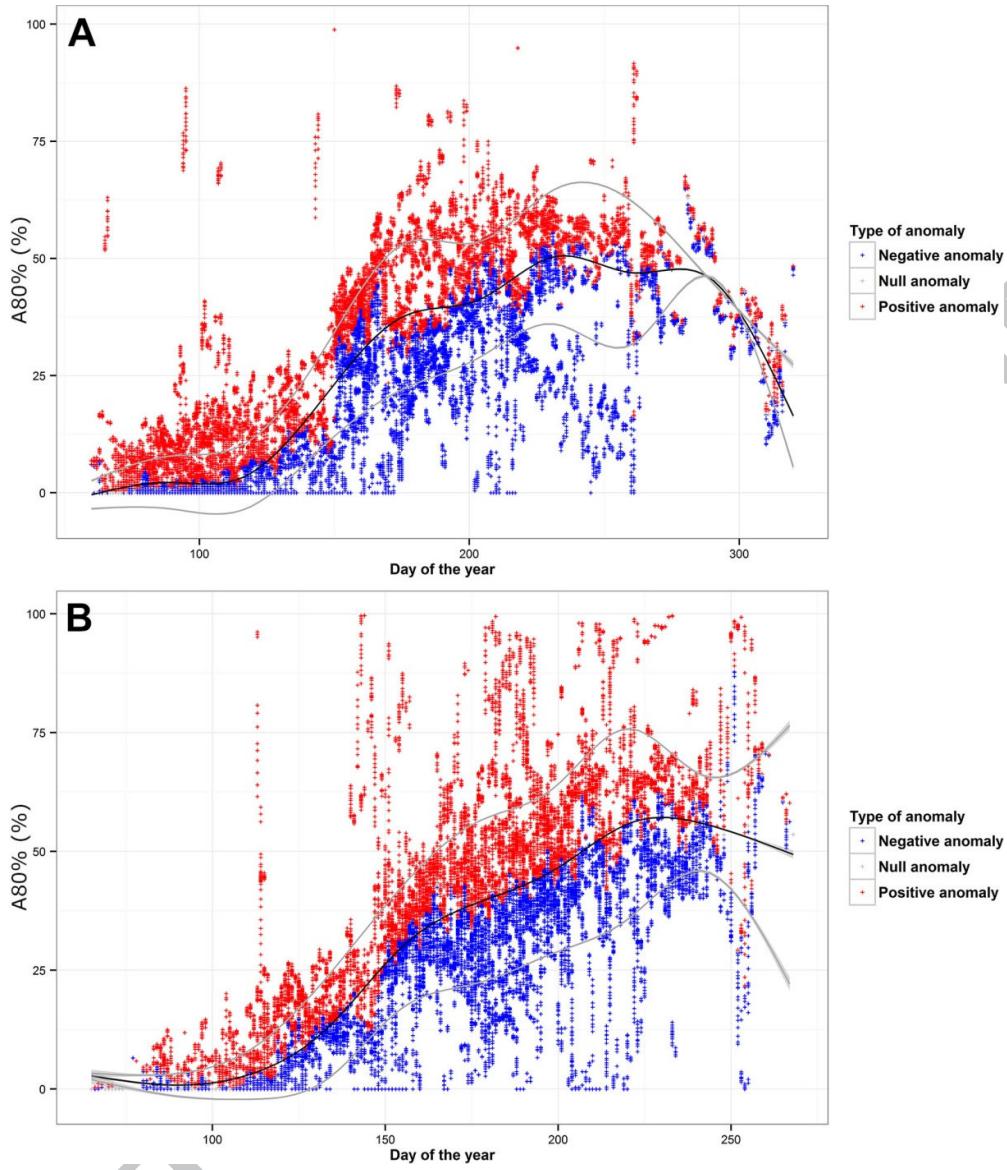
Appendix B

Computation of the anomaly of the spatial variability, $A'_{80\%}$: From March to August-September, an increase of $A_{80\%}$ with time was observed for males and females (Figure 1A - B); we defined $A'_{80\%}$ by (i) computing the median of the observations from the time-series of $A_{80\%}$ for males and females (black lines, Figure 1A – B), (ii) removing this median from each observation to obtain the anomaly of the spatial variability from its seasonal cycle (hereafter denoted $A'_{80\%}$).

Fig 1. Time series of $A_{80\%}$; the area covered by sea ice with concentration above 80% within a 50 km radius around the animal) for A) males and B) females. The time-series only includes positions inside the sea ice from March to the end of post-moult trips. The black line represents the median of the observations (used to compute the anomaly of the spatial variability from its seasonal cycle; $A'_{80\%}$), and grey lines represent the standard deviation associated with the median. Red dots correspond to positive local anomalies (observations superior to the median) while blue dots correspond to negative local anomalies (observations inferior to the median).

ACCEPTED MANUSCRIPT

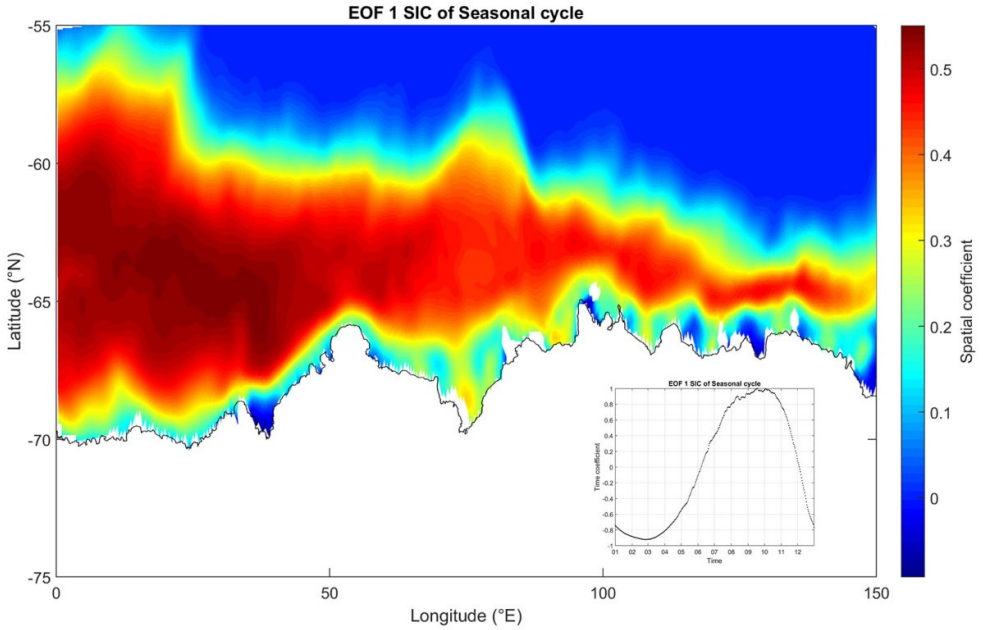
ACCEPTED MANUSCRIPT



ACCEPTED MANUSCRIPT

Appendix C

Fig 1. Description of the seasonal signal of sea ice concentration within the study area represented by the spatial and temporal pattern from an Empirical Orthogonal Function analysis over a 7 year time-series of sea ice concentration.

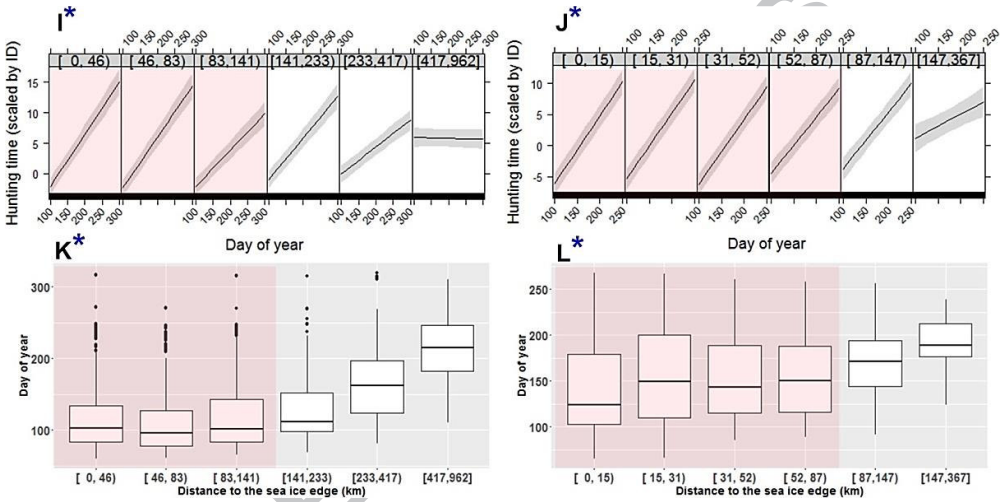


ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

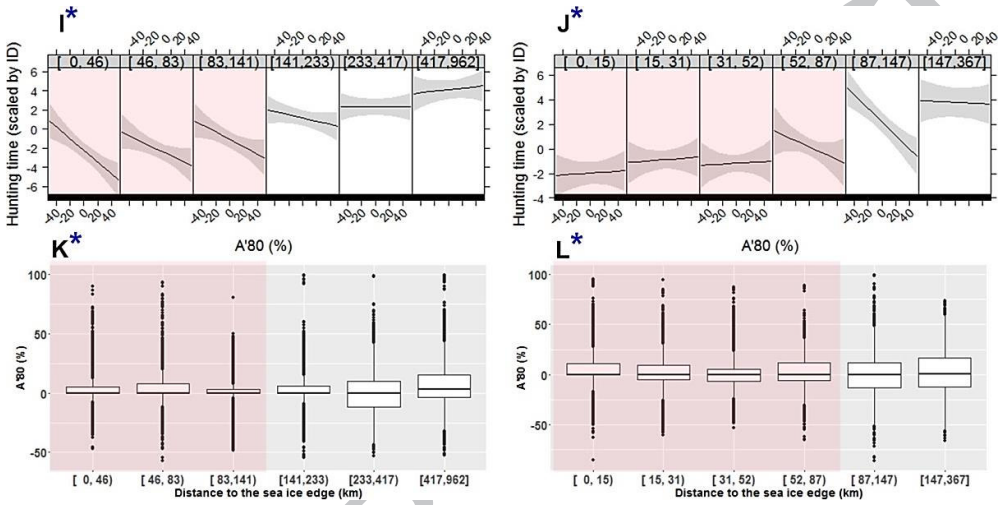
Appendix D

Fig 1. Model 2, relationships from the two LMMs between hunting time and the same variables used in model 1 (Figure 8) except the spatial variability of concentrated sea ice patches ($\mathcal{A}_{80\%}$) was replaced by the day of year. We choose to present only results for the modified variable as results are identical for other variables. Results for males are presented on the left panels and those for females on the right. Each graph from models shows the relationship relative to bin of the distance of the animal from the sea ice edge when inside sea ice (in km). For each graph, the thick lines represent the predictive values from the population at a given position in sea ice and the grey shaded envelopes represent the boundaries of the variation between the predicted values per individual. Available data for each bin of distance are represented by boxplots. The marginal ice zone is shown by the red shaded area.



ACCEPTED MANUSCRIPT

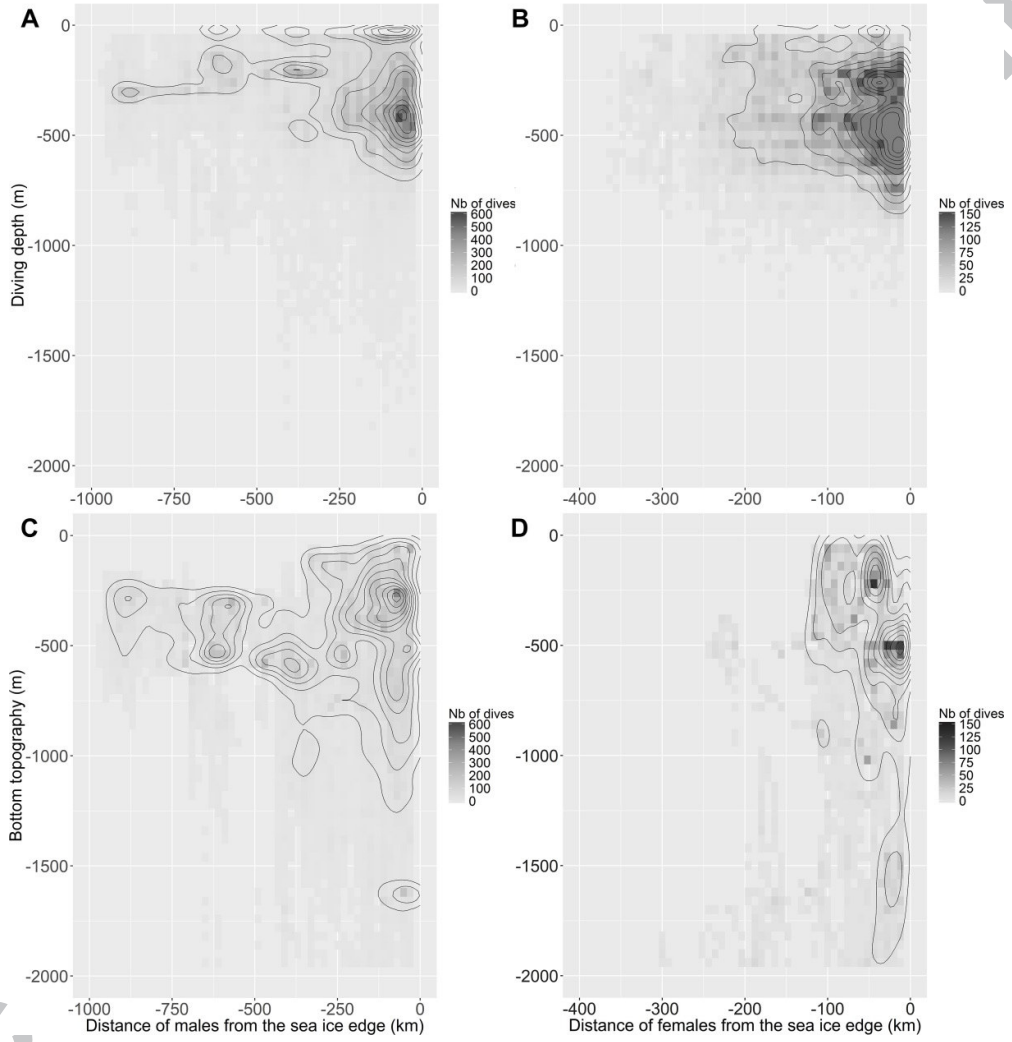
Fig 2. Model 3, relationships from the two LMMs between hunting time and the same variables used in model 1 (Figure 8) except the spatial variability of concentrated sea ice patches ($\mathcal{A}_{80\%}$) was replaced by the anomaly of the spatial variability of concentrated sea ice patches ($\mathcal{A}'_{80\%}$). We choose to present only results for the modified variable as results are identical for other variables. Results for males are presented on the left panels and those for females on the right. Each graph from models shows the relationship relative to bin of the distance of the animal from the sea ice edge when inside sea ice (in km). For each graph, the thick lines represent the predictive values from the population at a given position in sea ice and the grey shaded envelopes represent the boundaries of the variation between the predicted values per individual. Available data for each bin of distance are represented by boxplots. The marginal ice zone is shown by the red shaded area.



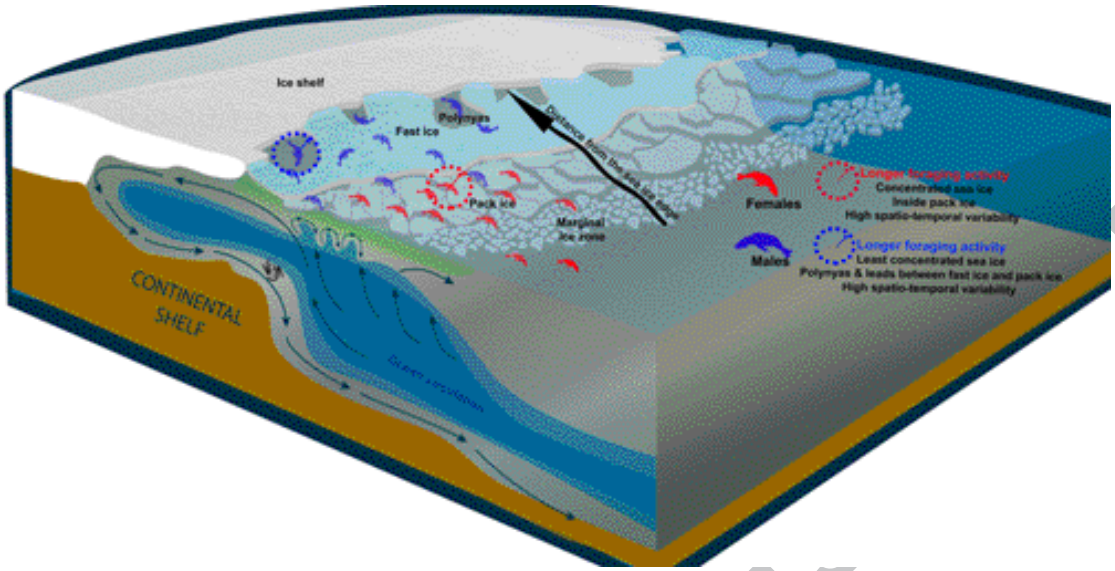
ACCEPTED MANUSCRIPT

Appendix E

Fig 1. Plot of diving depths (m) and bottom topography under the position of A & C) males and B & D) females relative to their distance from the sea ice edge (km) using a 2D kernel density estimation (*kde2D* function from package MASS, from R Development Core Team). One contour is drawn every 25 dives for females and 100 dives for males.



ACCEPTED MANUSCRIPT



ACCEPTED MANUSCRIPT