

Limited use of sea ice by the Ross seal (*Ommatophoca rossii*), in Amundsen Sea, Antarctica, using telemetry and remote sensing data

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Abstract To understand the use and importance of the Antarctic sea ice to the Ross seal (*Ommatophoca rossii*), four adult females were tagged with Argos satellite transmitters in the Amundsen Sea, Antarctica. The Ross seal is the least studied of the Antarctic seal species and nothing was previously known about their behaviour in the Amundsen Sea. During almost 1 year, their movements, haul out behaviour and time spent at different temperatures were logged. By comparing their movements with daily ice maps, distances to the ice edge were calculated, and seals dependence on sea ice for resting, breeding and moulting was analysed. The tagged seals spent on average 70.8 %

(range 66.8–77.8 %) of their time in the water and hauled out mainly during the moult in December–January, and in late October–mid-November during breeding. During the pelagic period, they were on average 837.5 km (range 587–1,282 km) from the ice edge indicating a fully pelagic life during several months. Their pelagic behaviour suggests that Ross seals, although being an ice obligate species, may adapt comparatively easy to climate change involving ice melting and recession and thereby potentially being less sensitive to the reduction of sea ice than other Antarctic seal species. Although nothing is known about their mating behaviour, they appear to be relatively stationary during moulting and breeding, hence requiring a small ice surface. Although previous studies in other parts of Antarctica have found similar results, still many questions remain about this peculiar species.

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Introduction

The Ross seal (*Ommatophoca rossii*) is the only species of the genus *Ommatophoca* and the least studied Antarctic seal. It was discovered in 1840 during the British Antarctic Expedition on board the vessels *HMS Erebus* and *HMS Terror* (1839–1843), lead by James Clark Ross and scientifically described by Gray in 1844 (Gray 1844, 1875; Kooyman and Kooyman 2009). Fewer than 50 sightings were reported prior to 1940 and only 200 sightings before 1972 (Hofman et al. 1973). The species is listed as ‘Lower Risk, Least Concern’ by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species

Version 2012.2 (Southwell 2008), based on its widespread occurrence and large population size. Hence the species is not dependent on conservation measures, but it has been designated as a protected species since 1972 in the Annex two of the convention for the conservation of Antarctic seals (adopted under the Antarctic Treaty—1959) as a measure for the conservation of Antarctic fauna and flora, and since 1998 as a specially protected species due to deficient available information.

Ross seals have a circumpolar distribution (Bengtson et al. 2011) and have previously been assumed to be confined deep in the Antarctic pack ice zone, probably due to the paucity of the observations, caused by the difficult access to their habitats (Hofman et al. 1973; Skinner and Klages 1994; Blix and Nordøy 2007). Up until recently little was known about this species distribution, abundance, life history and behaviour compared with the other Antarctic phocids. However, recent tagging studies showed that Ross seals display pelagic behaviour during most of the year (Blix and Nordøy 1998, 2007) and can reach latitudes of the South Sandwich, Falkland, Scott, South Orkney, Kerguelen, Heard Islands and South Australia as vagrants (Thomas and Rogers 2009). Therefore, Ross seals are considered *commuters*, as they are ice-dependent for breeding, but forage in lower latitudes far away from the heavy pack ice (Kooyman and Kooyman 2009). However, the movements of the Ross seals in relation to the ice edge have never been examined.

In the present study, we provide information on the location, distance to ice edge, time spent in regions with different temperatures and haul out behaviour of four adult female Ross seals tagged with Argos satellite transmitters. Our aim is to examine the correlation between Ross seal movements and the position of the seasonal Antarctic ice edge.

Materials and methods

Study area

The study was conducted in the Amundsen Sea (Fig. 1) from the Swedish icebreaker Oden. The abyssal plain in the Amundsen Sea has a depth of about 5,000 m. To the north of Marie Byrd Land, a chain of seamounts extends between 68–70°S and 115–130°W and raises up to depths of about 1,000 m (Kurentsova et al. 2008). The continental shelf in the Amundsen Sea, between 100°W and 135°W and south of 71°S, extends from 100 to 200 km west of Siple Island (73°51'S, 125°50'W) to >400 km north of Pine Island Bay (75°10'S, 100°0'W). It has an average depth of 500 m and is characterized by a number of deep (glacially scoured) troughs leading from the shelf break to the deeper

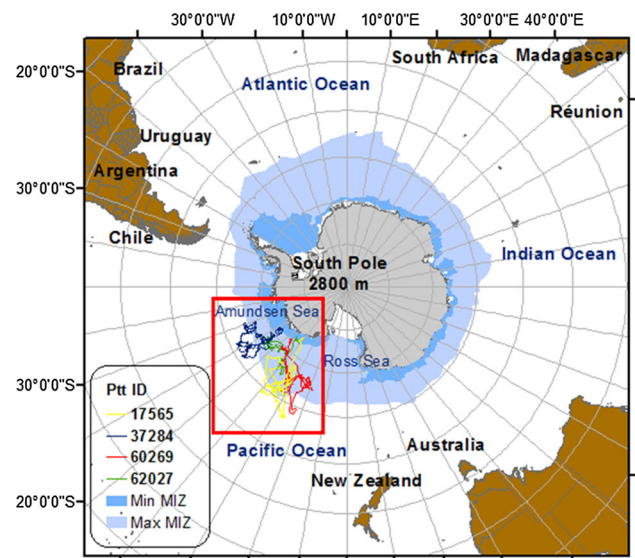


Fig. 1 Map of the study area, showing the movements of four Ross seals (*Ommatophoca rossii*) tagged with Argos transmitters and tracked from late December 2010 to early December 2011. Minimum marginal ice zone (MIZ) (dark blue) at the end of February 2011 and maximum marginal ice zone (light blue) at the end of September 2011 are illustrated

(>1,000 m) inner shelf basins (Arndt et al. 2013). The shelf break is steep and drops off rapidly to depths exceeding 3,000 m (Arndt et al. 2013). The Antarctic Circumpolar Current (ACC), which carries water eastward around the continent, has an average flow path running unusually close to the shelf break in the Amundsen Sea compared with other Southern shelf areas (Orsi et al. 1995). Warm deep water is present on the seabed and flows towards the coast in the deep troughs (e.g. Walker et al. 2007; Wåhlin et al. 2010), possibly aided by the proximity of the ACC (Wåhlin et al. 2012).

The ice cover in the Amundsen Sea during minimum ice extent (February–March–April) extends on average to about 70°S, and maximum ice extent on average at about 65°S with substantial annual variability. In a few southern parts, land-fast perennial ice cover is present. There are also two coastal polynyas: the Pine Island Polynya and the Amundsen Polynya (Aubail et al. 2011). Small parts of the polynyas stay open during winter, but in summer, they grow to cover about half the continental shelf (sometimes all of it; Arrigo et al. 2012). The region contains a large number of travelling as well as stranded ice bergs, which calve off from the numerous floating glaciers (ice shelves) at the coast. The vulnerability of these ice shelves and their importance for the fate of the West Antarctic Ice Sheet have been discussed in numerous recent publications (e.g. Pritchard et al. 2012; Rignot et al. 2013).

During the study period, the ice extent in the Amundsen Sea was at its minimum during the end of February 2011

(around 70°S) and at its maximum at the end of September (around 65°S).

Primary productivity in the Amundsen Sea (Southern Ocean) is among the highest in Antarctica, and it is probably enhanced in the two polynyas due to iron availability from glacial meltwater formed as warm deep water that comes in contact with the ice shelves and/or ice bergs (Walker et al. 2007; Wåhlin et al. 2010). There is a peak of phytoplankton bloom around January (Chl a concentration of 4 mg/m³ in PIP and 7 mg/m³ in AP; Arrigo et al. 2012), which may provide resources for apex predators such as seals, cetaceans and penguins (Ackley et al. 2003).

Capturing and tagging

Four female Ross seals were caught in the Amundsen Sea on 29 December 2010 and 2, 3 and 4 January 2011, respectively. All four seals were physically and sexually mature females according to weight-based age estimation from the literature (Skinner and Klages 1994; Nordøy and Blix 2002; Blix and Nordøy 2007; Thomas and Rogers 2009; Table 1). The lengths of the animals are not comparable with the measurements in the above studies since seals in our study were not anesthetized during the tagging procedure and therefore contracted during measurements—anesthetized animals are completely relaxed and thus longer.

All four animals were at the late stage of moulting with new fur on the head and extremities and loose hair on the rest of the body. Three of the satellite transmitters were glued to the new pelage of the seal's head in order to maximize the probability for uplinks to the satellite when the seal was at the surface. The fourth transmitter was glued to the neck, after removing loose hair, as the transmitter dimensions were too big to be attached on the head.

The seals were spotted during surveys from a helicopter. After landing on the ice within 100–500 m, the seals were caught using a lightweight pole-net made with carbon fibre wind surfer masts and 2 × 2 cm nylon net. The seals did not react to the helicopter and did not try to escape when they were approached. A small hole was cut in the pole-net at the place of the transmitter, and the seal was physically restrained while the glue was hardening (Araldite 2012, 2-component quick setting epoxy). The tagging procedure followed Fedak et al. (1983). The seals were measured and weighed during ventral recumbency using a lightweight tripod and a digital scale (Salter). Blood samples, a skin biopsy and hair samples were also collected. The whole operation took <1 h per seal.

Details of the tagged seals are shown in Table 1. The four seals will from here on be referred to as: 17565 (Yellow), 37284 (Blue), 60269 (Red) and 62027 (Green), referring to colours used in the figures.

Table 1 Basic biological and tagging information from the four Ross seals (*Ommatophoca rossii*) tagged in December 2010 or January 2011 in Amundsen Sea, Antarctica

PTT id	17565 (yellow)	37284 (blue)	60269 (red)	62027 (green)
Sex	F	F	F	F
Length (cm)	187	182	196	196
Weight (kg)	192	145	198	205
Age class	adult	adult	adult	adult
Type of transmitter	SPOT5 (2xC-cells)	SPOT2 (2xM1 cells)	SPOT5 (1xM1 cell)	SPOT5 (1xM1 cell)
Information provided by tags				
Location	yes	yes	yes	yes
Time at temperature	yes	no	yes	yes
Haul out	yes	no	yes	yes
Position of tag on seal	neck	head	head	head
Date of deployment.	4 January 2011	29 December 2010	2 January 2011	3 January 2011
First signal	8 January 2011	29 December 2010	2 January 2011	3 January 2011
Last signal	27 November 2011	25 October 2011	3 December 2011	26 July 2011
PTT longevity (days)	323	300	335	204
Number of location days	231	284	149	89
Duty cycle (days to transmit)	every day	every day	every day from 1–31 January; every other day February–December	every day from 1–31 January; every other day February–July
Maximum number of trans./d	500	200	200	200
Travelled distance(∑km between best daily locations)	11481	10,395	11220	5,895

Three types of Argos transmitters were used: three of them were SPOT5 tags measuring either $3.8 \times 1.8 \times 1.7$ cm, 28 g (two tags with 1xM1 battery providing $\sim 30,000$ transmissions) or $16.4 \times 3.9 \times 3.4$ cm, 260 g (one tag with 2xC-cell batteries providing $\sim 120,000$ transmissions, Wildlife Computers, Seattle, WA, USA); the fourth tag was a SPOT2 measuring $4.5 \times 1.1 \times 4.0$, 49 g (2xM1 batteries providing $\sim 60,000$ transmissions, Wildlife Computers, Seattle, WA, USA). Tags were duty cycled to transmit every day or every second day and programmed to transmit 200–500 times per duty day to the Argos satellite system aboard the NOAA polar orbiting satellites (CLS/Service Argos, www.argos-system.org). A conductivity sensor (saltwater switch) limited transmission to periods when the device was out of the water. The interval between transmissions when the seals were at surface at sea was one transmission every 45 s and when hauled out 90 s. The hours to transmit for all of the tags were 12–21 h (GMT).

Data collection and analysis

SPOT5 tags collected locations, time at temperature histograms (TAT) and haul out timelines in 24-h bins. The SPOT2 tag collected only locations.

The location of the instrumented seals was determined by the Argos system. Nevertheless, Argos locations have a not easily determined uncertainty of a few metres to several kilometres for latitude and longitude that may affect the biological interpretation of the data (Douglas et al. 2012).

To increase accuracy and reliability of the data, we first excluded invalid location [Location Class (LC) Z, 6.3 % of the original Argos data]. All remaining positions were filtered by the default Kalman filter provided by Argos. In order to further improve the data accuracy and remove implausible locations, a SAS-routine filter was applied (Argos-Filter v7.03, Douglas 2006, USGS/ASC). The SAS-filter settings were as follows: distance between locations (maxredun) of 2 km, maximum swim speed (minrate) of 10 km/h, and angle between consecutive vector lines from the previous and following location of 10° . For further information on these parameters, see Online Resource 1.

The SAS-filter routine was programmed to automatically select the most accurate location each day, based on the Argos Location Class and the number of uplinks per transmission (Douglas 2006). Resulting locations and the percentage of removed locations and class locations of all retained locations are provided in Table a of Online Resource 1.

The telemetry data were imported into and visualized in ArcGIS 10.1 (ESRI). All the geographical information was mapped with South Pole Stereographic coordinate system, Stereographic projection and World Geodetic System 1984 datum (WGS84).

Time at temperature (TAT)

TAT is the proportion of time that the seal spent at one of the 12 user-specified temperature ranges taken at 10-s intervals regardless of whether the seal is diving or hauling out and summarized into 4-h bin periods (see Table 2 for values selected in this study).

TAT data were collected from the three SPOT5 tags with a total of 2801 4-h histograms for the periods 0.00–4.00, 4.00–8.00, 8.00–12.00, 12.00–16.00, 16.00–20.00 and 20.00–0.00 h (GMT) during 268 days for seal Yellow, 305 days for seal Red and 173 days for seal Green, more than 80 % of the days that the PTTs were active.

Haul out

The haul out is measured as the percentage of each hour the tag's wet/dry sensor indicates 'dry'. It varies between 0 and 100 % with intervals of 10 % between 5 and 95 % and 5 % between 0 and 5 % and 95 and 100 %. A value of 0 % means that the sensor was always wet during that hour (diving or shallow swimming with only the nose clearing the surface of the water); 10 % means that during that hour, the sensor was dry for 6 min; 50 % means 30 min (e.g. the seal was swimming at the surface); and 100 % means that the seal hauled out during that hour or in the unlikely event that the seal had its head out of the water for a full hour. Haul out data were corrected into local solar time depending on the geographical location of the seal at that time (Burns et al. 2004).

Haul out data were collected from the same three seals during an average of 142 24-h periods for each seal, (range 102–176 days) from January 2011 to November 2011, almost 50 % of the days that the PTTs were active.

Table 2 User-specified temperature bins for the TAT (Time at Temperature) sensor that were summarized over 4-h periods

Temperature range (°C)	
1	–40.0 to –30.0
2	–29.9 to –20.0
3	–19.9 to –10.0
4	–9.9 to –5.0
5	–4.9 to –2.0
6	–1.9 to –1.0
7	–0.9 to 0.0
8	0.1 to 1.0
9	1.1 to 2.0
10	2.1 to 3.0
11	3.1 to 4.0
12	4.1 to 60.0

Distance to sea ice edge and bathymetry

Information on daily sea ice edge in Antarctica was provided by the US National Ice Center, Naval Ice Center, available online at: http://www.natice.noaa.gov/Main_Products.htm.

The maps are constructed by NIC using several imagery sources with resolutions down to 50 m per pixel. Imagery sources include but are not limited to ENVISAT, DMSP OLS, AVHRR and RADARSAT.

Bathymetry was obtained from the International Bathymetric Chart of the Southern Ocean (IBCSO) Version 1.0—A new bathymetric compilation covering circum-Antarctic waters, available online <http://www.ibcso.org/> (Arndt et al. 2013).

Daily seal locations (based on the best position per day) were mapped together with the daily ice edge position, and the smallest distance between seal and ice edge was analysed.

Seal movement

The movements of the tagged seals were divided into seven periods with similar patterns in direction and swimming speed during the tracking period from late December 2010 to early December 2011.

Results

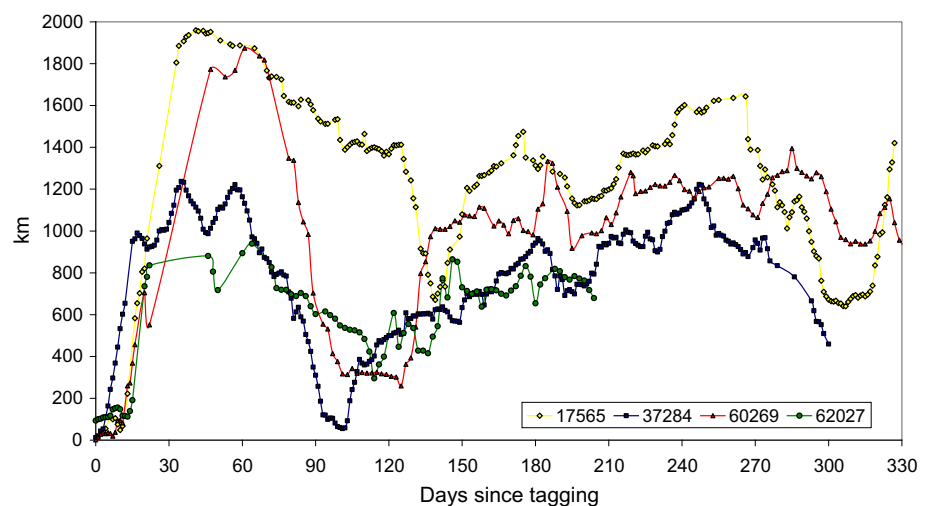
Seals' movement

The seals were caught and tagged in the Amundsen Sea at the end of December and beginning of January. The general pattern in distance that moved from the tagging site during the year appears to be very similar for the four seals,

although somewhat shifted in time and maximum distance to the tagging site (800–2,000 km, Fig. 2). The movements of each seal (Fig. 3) was divided into seven time periods of the year showing a common pattern of direction and speed, although time periods may have different starting dates for the different seals (Table 3).

- (1) *Late December to early January* During the first days after tagging (4–11 days), the seals remained around the tagging area (average distance to deployment site 104 km, range 54–156 km), with a low swimming speed or potentially sea ice drifting speed, as they spent most of the time on the ice (average 0.72 km/h, range 0.54–0.84 km/h).
- (2) *Mid-January to late January* The seals headed north with a high speed (average 3.12 km/h, range 2.74–3.58 km/h), over twice the average rate for all other periods. They moved at least between 900 km (seals Blue and Green) to 2,000 km (seals Yellow and Red) during this period (25, 11, 36 and 11 days for seals Yellow, Blue, Red and Green, respectively).
- (3) *Late January–early February to mid-March* The seals stayed in these northern latitudes for over a month, reaching the furthest point from the deployment site (1,960, 1,237, 1,874 and 940 km for seals Yellow, Blue, Red and Green, respectively) and the lowest latitude (56.608, 61.064, 58.348 and 64.556°S, respectively). That means that two of the four seals moved out of the jurisdiction of the Antarctic Treaty System which applies to the area south of 60°S.
- (4) *Mid-March to late April–mid-May* In this period, all seals travelled back towards the south/south-east during more than 1 month (2 months in case of Yellow) until they reached the vicinity of the tagging

Fig. 2 Distance from each position to the tagging site (day 0) until the last day with transmission (27 November 2011, 25 October 2011, 3 December 2011 and 26 July 2011 for seals Yellow, Blue, Red and Green, respectively)



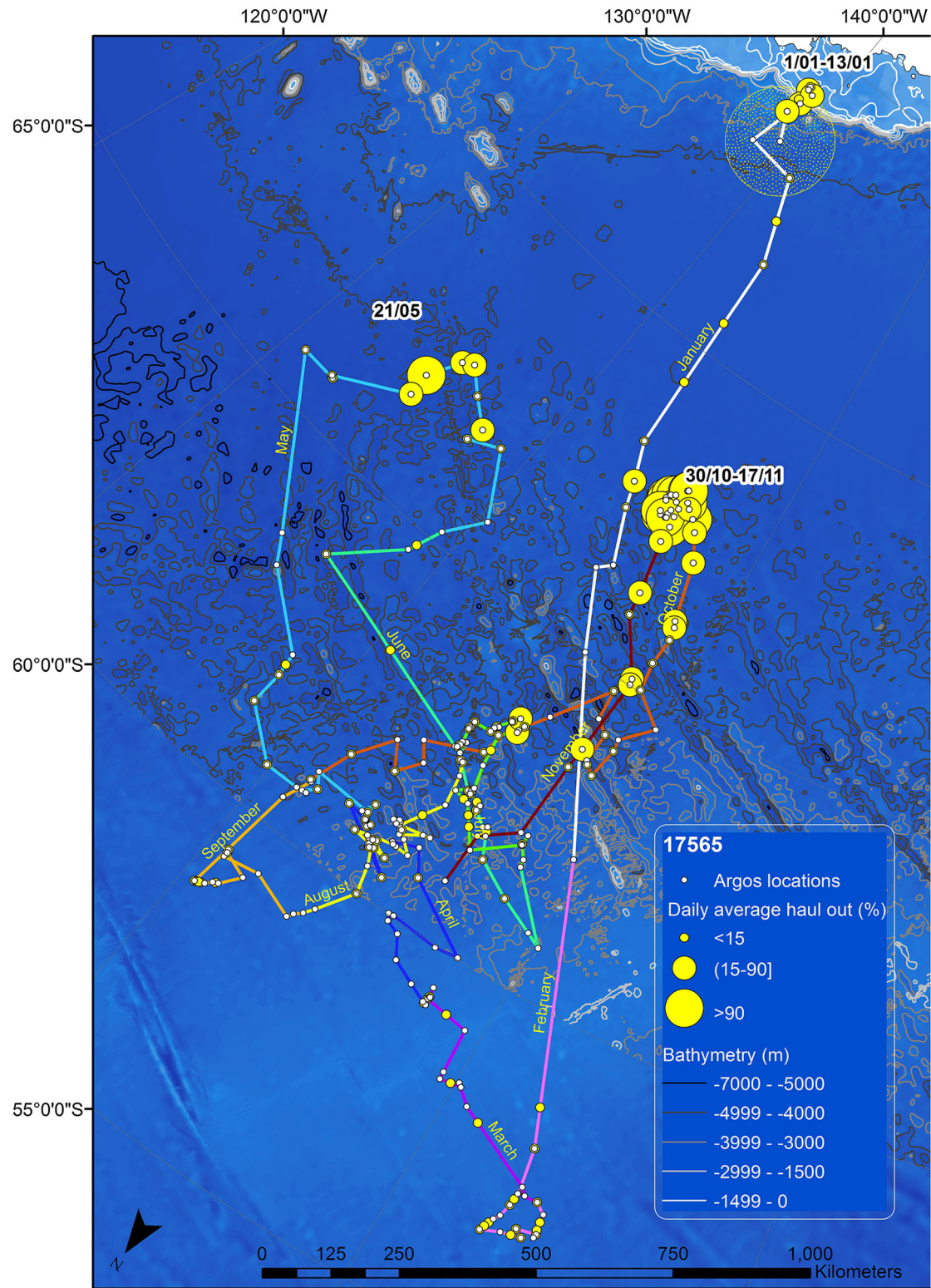


Fig. 3 Map showing the daily average haul out time (only available in the three SPOT5 satellite tags) combined with the seal trajectory obtained from the best position per day. New points have been added along the track when Argos location was missing for a particular date, in order to display the entire haul out information received from the satellite. The new dates were added evenly spaced based on dates

missing and the received Argos positions (29 new points for seal Yellow, 100 for seal Red and 57 for seal Green). Original Argos locations are shown with white points. The size of the coloured points is proportional to the percentage of time hauling out. Information about the haul out histogram is also added. Polar stereographic map projection, WGS84

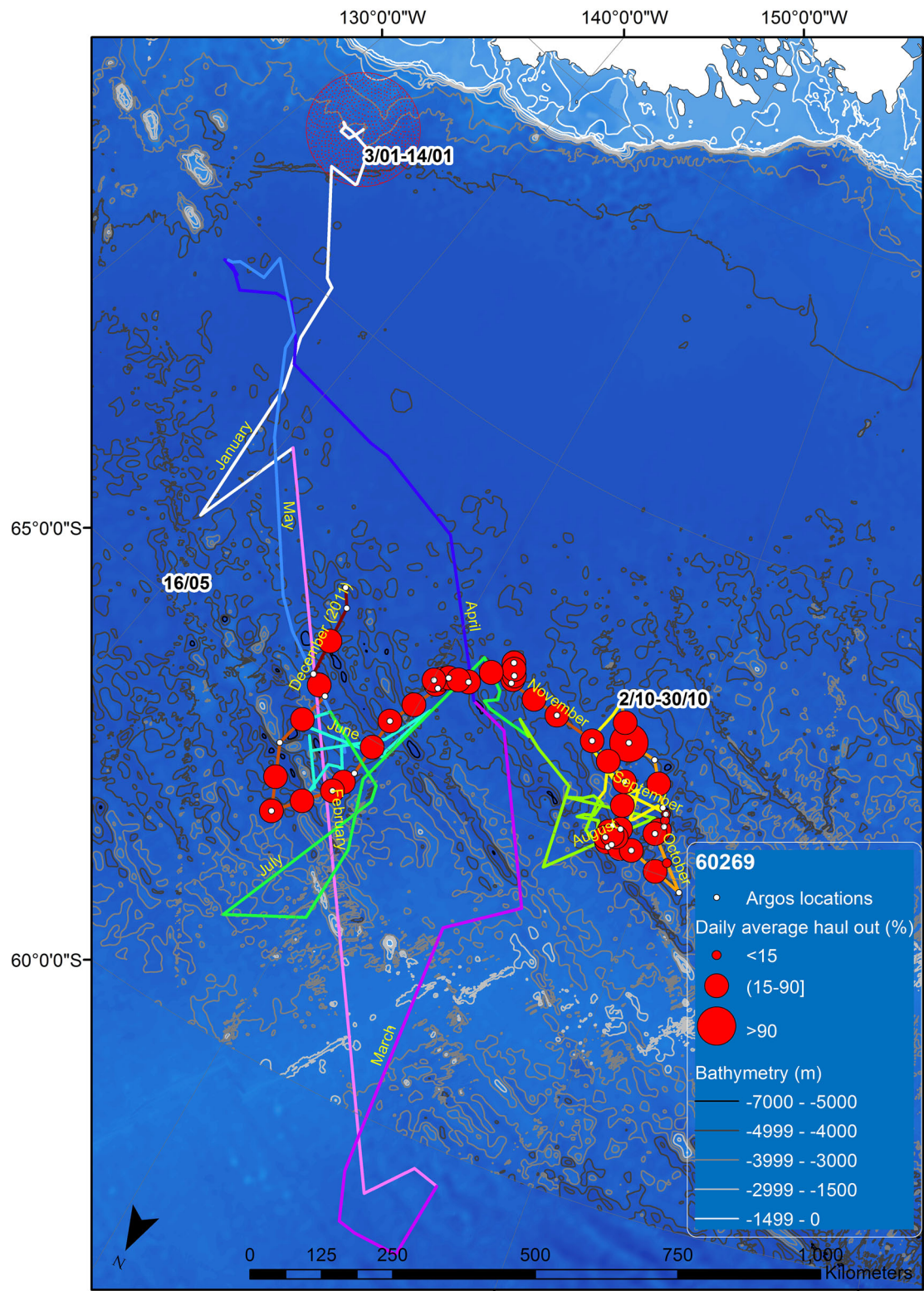


Fig. 3 continued

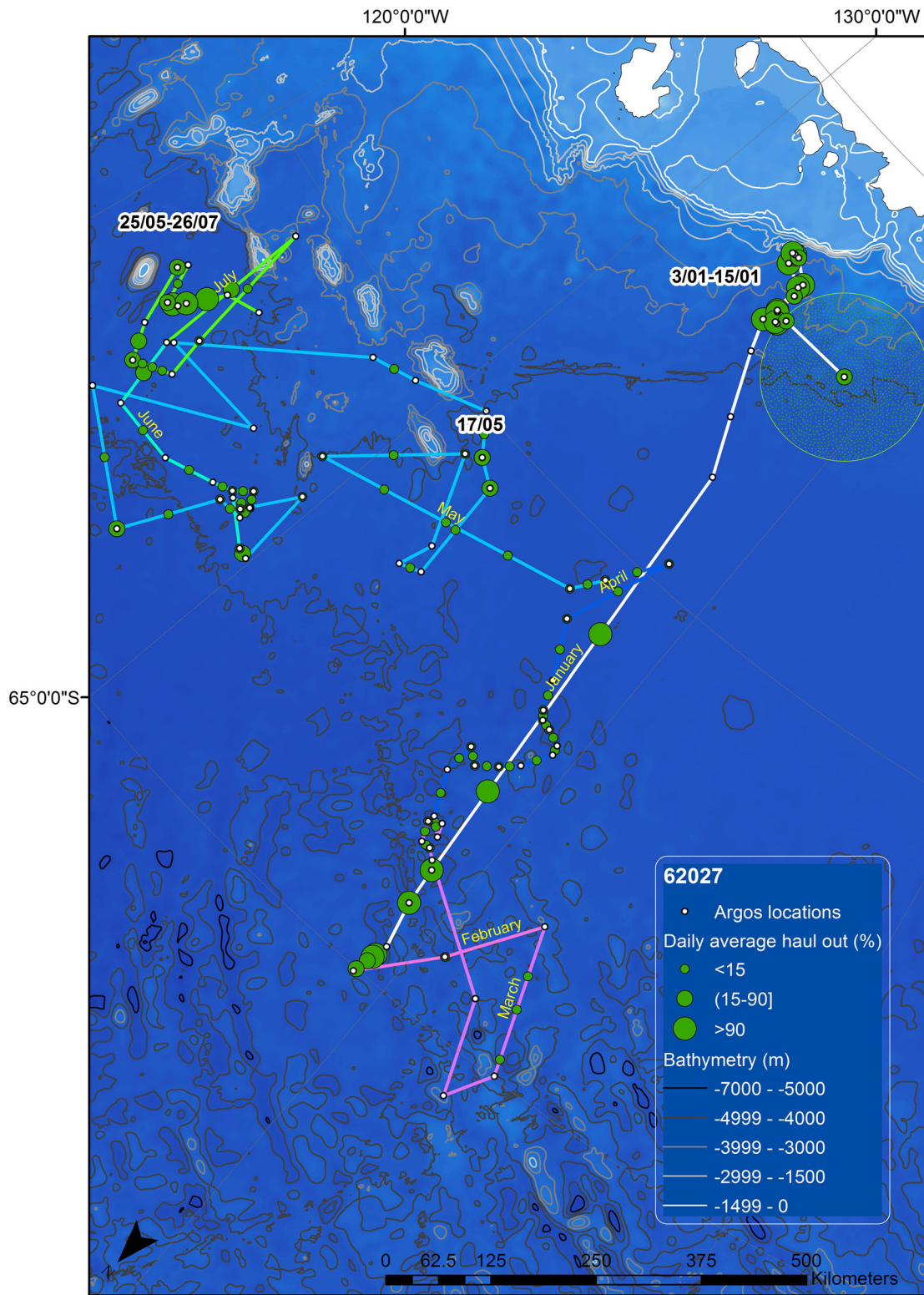


Fig. 3 continued

Table 3 Details of duration (elapsed days), swimming speed and distance moved in the seven movement phases for the four seals

		17565 (yellow)	37284 (blue)	60269 (red)	62027 (green)
Phase 1. Around tagging site	Date	1/4/2011	12/29/2010	1/2/2011	1/3/2011
	Elapsed days	10	5	12	12
	Rate of movement (km/h)	0.84	0.69	0.82	0.54
	Travelled distance (km)	173	57	245	244
Phase 2. First and quick travel to the north	Date	1/14/2011	1/3/2011	1/14/2011	1/15/2011
	Elapsed days	25	11	36	11
	Rate of movement (km/h)	3.58	3.11	3.06	2.74
	Travelled distance (km)	2,072	952	2,089	907
Phase 3. The farthest and lowest latitude point	Date	2/8/2011	1/14/2011	2/19/2011	1/26/2011
	Elapsed days	31	41	24	50
	Rate of movement (km/h)	0.68	1.40	0.90	1.13
	Travelled distance (km)	348	1,376	455	625
Phase 4. Coming back to the south a	Date	3/11/2011	2/24/2011	3/15/2011	3/17/2011
	Elapsed days	60	38	30	36
	Rate of movement (km/h)	1.30	1.64	2.49	0.64
	Travelled distance (km)	1,733	1,550	1,710	534
b	Date	5/10/2011	4/3/2011	4/14/2011	4/22/2011
	Elapsed days	14	8	24	6
	Rate of movement (km/h)	3.17	0.64	0.57	1.67
	Travelled distance (km)	1,092	123	327	240
Phase 5. To the north, mid-latitudes	Date	5/24/2011	4/11/2011	5/8/2011	4/28/2011
	Elapsed days	127	146	160	89
	Rate of movement (km/h)	1.28	1.34	1.36	1.54
	Travelled distance (km)	3,324	4,741	4,843	3,345
Phase 6. Back heading south	Date	9/28/201	9/4/2011	10/15/2011	
	Elapsed days	41	51	24	–
	Rate of movement (km/h)	1.94	1.41	1.07	–
	Travelled distance (km)	1792	1594	616	–
Phase 7. Last travel to the north	Date	11/8/2011		11/8/2011	
	Elapsed days	19	–	25	
	Rate of movement (km/h)	1.97	–	1.48	
	Travelled distance (km)	174	–	934	
Entire period	Rate of movement (km/h)	1.63	1.43	1.38	1.31
	Travelled distance (km)	11,481	10,395	11,220	5,895

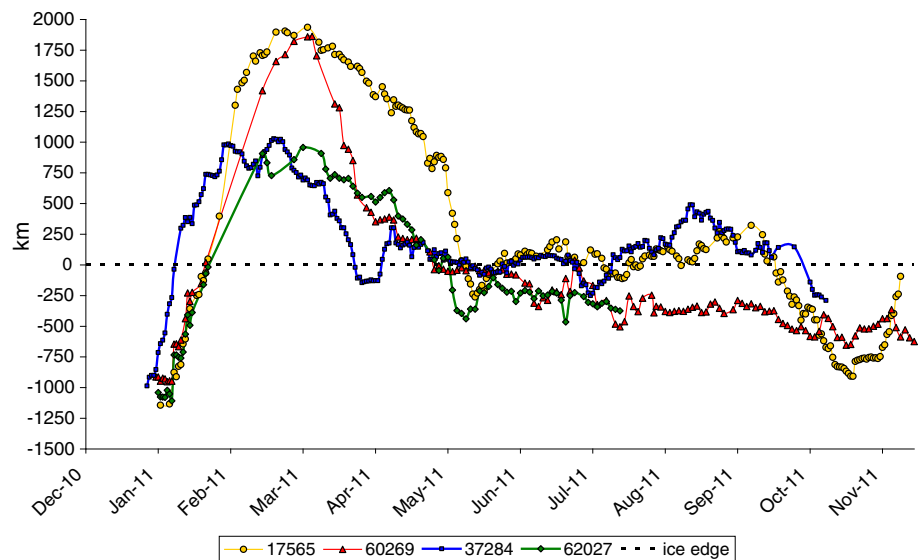
site (except for seal Yellow that remained 670 km to the north).

- (5) *Late April–mid-May to late September–mid-October* The seals headed back north again remaining in mid-latitudes (60–63°S for Yellow, 63–67°S for Blue, 64–66°S for Red and 60–62°S for Green) for almost 4 months (2.5 months for seal Green until the tag failed after 204 days). The swimming speed was slightly lower (1.38 km/h, range 1.28–1.54 km/h) than the average rate for all of the periods (1.44 km/h, range 1.31–1.63 km/h).

- (6) *Late September–mid-October to late October–mid-November* The seals headed south again to southern latitudes (67–68°S). The average swimming speed was similar (1.47 km/h, range 1.07–1.94 km/h) to the average rate for all periods. After 300 days of transmission, the tag Blue stopped.

- (7) *Late October–mid-November to late November–early December* The two remaining seals (Yellow and Red) headed north again into the mid-latitudes in phase five. After 327 days, the Yellow tag stopped. For the last 4 days, seal Red headed south again.

Fig. 4 Distance from each Ross seal location (one position per day) to the ice edge. Negative values show that the seals are in the pack ice, while positive values mean that they are in open water



This tag stopped transmissions 335 days after deployment.

During the study period, the seals travelled a total of 11,481 km (Yellow), 10,395 km (Blue), 11,220 km (Red) and 5,895 km (Green), with an average surface displacement of 33.15 km/day (range 28.90–35.55 km/day).

Distance to ice edge

The tagging site was deep in the pack ice, about 1,000 km from the ice edge. Until the mid/end of January, the seals moved around in the pack ice (Fig. 4). During the first days after tagging, the seals headed for the ice edge. Seal Blue reached the ice edge on the 10 January, and the other seals reached it later: on 24 January (Red) and 25 January (seals Yellow and Green, Figs. 4, 5). After reaching the ice edge, seals Blue and Green spent around 76 days in open water, while seals Yellow and Red spent 114 and 100 days in open water, respectively. Seals Yellow and Red reached the farthest distance from the ice, on 10 March, staying 1,936 and 1,863 km away from the ice edge, respectively. Seals Blue and Green reached a maximum distance to the ice edge of 1,029 and 958 km on 23 February and 8 March, respectively (Figs. 4, 5). No ice-class data were available which would have enabled us to identify any ice-class-related behaviour. It is noted, however, that the ice concentration goes from 0 to 100 % in a short distance and that the ice edge is very sharp (Fig. 5), suggesting that the seals are in pack ice or open water and not tend to remain in areas of scattered ice.

After returning to the ice edge, the seals remained within 500 km from the ice edge (often <250 km) from late April–early May to late September. From the beginning of October, seals Yellow and Blue went deep into the pack ice until the end of the study, while seal Red gradually moved

into the ice from mid-July. Thus, the seals Blue, Yellow and Green stayed on the pack ice only 23, 33 and 47 % of time, while seal Red stayed almost 70 % of time, and only during two periods, they stayed deep in the pack ice: in late December–early January and during October, both periods about 1,000 km from the ice edge (Figs. 4, 5).

Haul out behaviour

The haul out data (Figs. 3, 6) obtained from the three SPOT5 transmitters show that the seals spent, on average, 29.2 % of the time hauled out (range 22.2–33.2 %). The highest percentages of hauling out were observed at medium and high latitudes when they were deep into the pack ice or close to the ice edge. Seal Yellow showed the most pronounced pelagic behaviour with 77.8 % of the studied period in the water, which equals to 254 days. The daily percentage of haul out combined for each seal track is shown in Online Resource 2. Some common behaviour among the seals was noted and described below (numbers refer to the classification introduced in Sect. 3):

(1) *Early January*

Haul out was continuous or almost continuous for seals Red (3–14 January) and Green (3–15 January) with more than 85 % of the time on the ice. The first data for seal Yellow are from 8 January, as the tag only activated itself when it was in salt water. That means that since 4 January, when it was tagged, this seal remained hauled out continuously. Two of the three seals hauled out on some days while they travelled north.

(4) *Mid-May*

In mid-May, all three seals hauled out for one full day (21 May for seal Yellow, 16 May for seal Red and 17 May

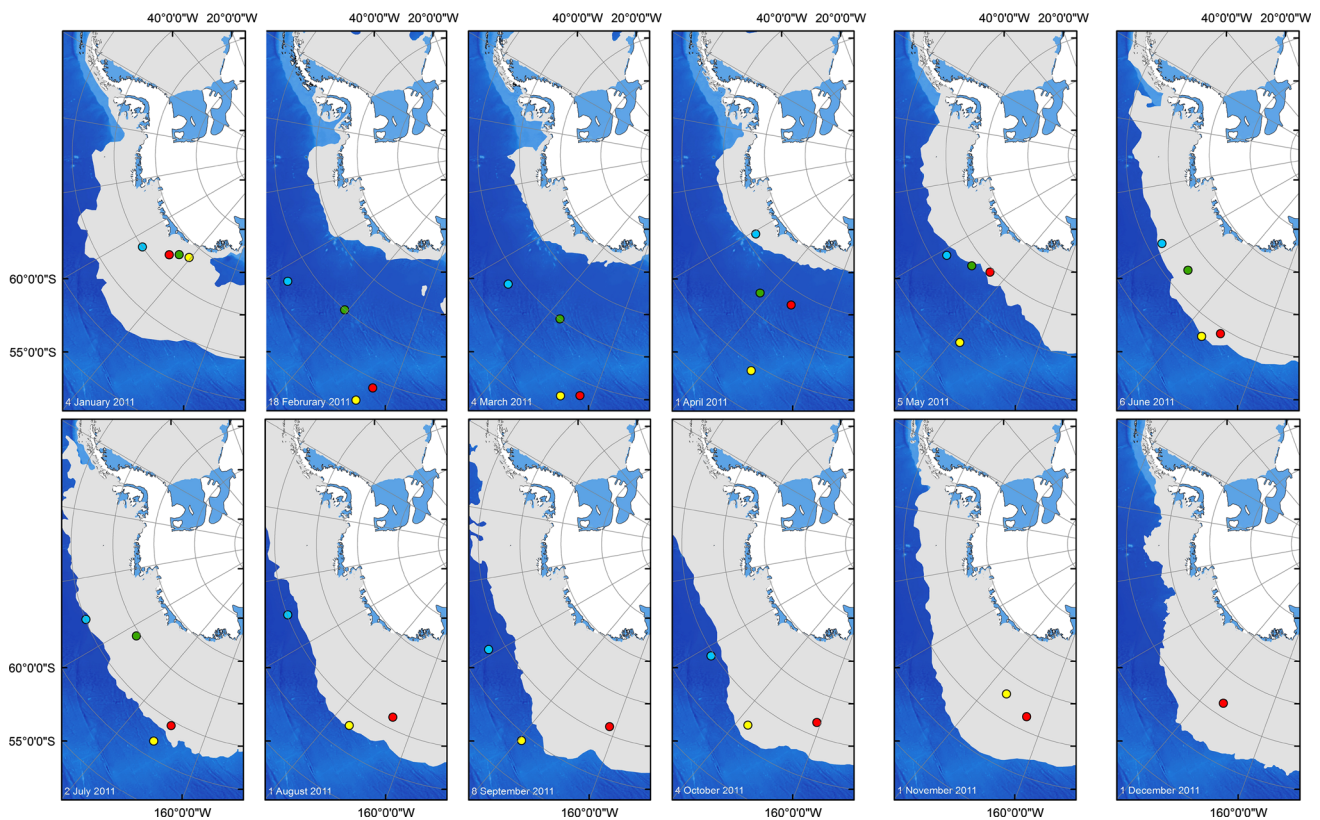


Fig. 5 Maps showing the monthly development of the pack ice edge (illustrated in *light grey*) in West Antarctica during 2011 and the positions of the four instrumented Ross seals. Seal location corresponds to the first date of each month where reliable locations were received from all seals. Daily ice edge around Antarctica has

been collected from the US National Ice Center, Naval Ice Center, for the same dates as the seal location. Seal Yellow (*yellow dots*) stopped transmitting the 27 November, seal Blue (*blue dots*) the 25 October, seal Red (*red dots*) the 3 December and seal Green (*green dots*) the 26 July

for seal Green) ending the long pelagic period (127 days for seal Yellow, 72 days for seal Red and 89 days for seal Green).

(5) July

In July, the seals' alternated days hauled out (partially) with days swimming most of the time, with an average of 5.50 % (Red), 16.86 % (Blue) and 38.43 % (Green) of time hauled out, respectively.

(7) October–mid-November

Seal Yellow hauled out continuously from 30 October to 6 November and near continuously with more than 90 % of the time on ice from 7 to 17 November, while seal Red hauled out an average of 35.26 % between early September until end of November, with a haul out peak around 2 October.

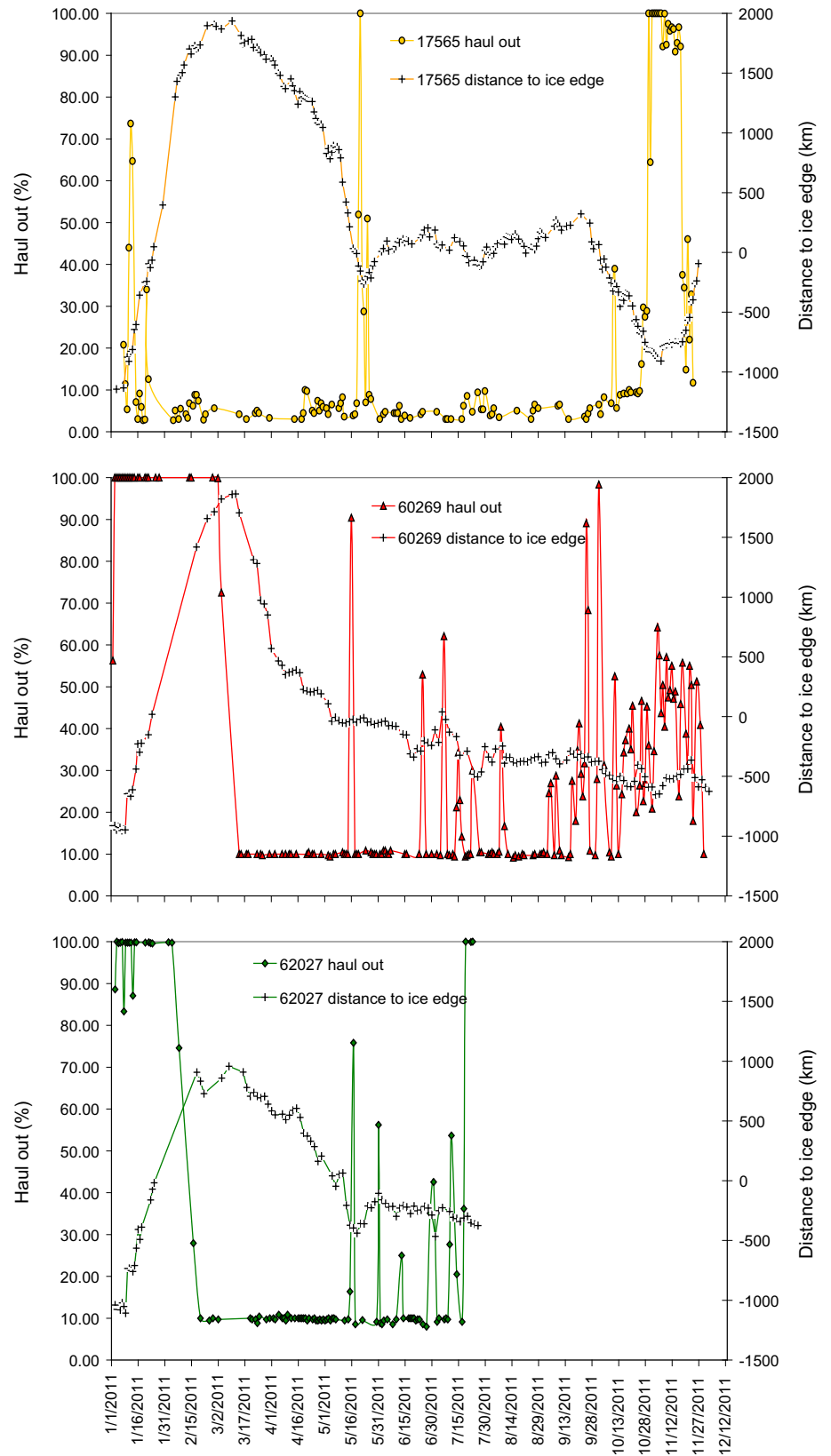
Figure 7 shows the diurnal variation of the haul out behaviour for different months. While seal Green hauled out almost continuously during January and seal Red hauled out continuously during both January and February, seal Yellow only spent up to on average 40 % of time on

the ice around midday (local time). In November, seal Yellow hauled out most of the time, without any clear diurnal pattern. Seal Red regularly hauled out during October–November with a clear diurnal pattern, peaking around solar midday.

By analysing the hourly distribution in detail of haul out during the moult between early January (week one) and the end of February (week eight), and during breeding also from mid-October (week 42) and the end of November (week 47), differences in behaviour for time of year as well as for individual seals were found (Online Resource 2).

While seal Red hauled out continuously until the first week of March and seal Green until mid-February, seal Yellow only sporadically hauled out for the first 3 weeks of January and mainly during midday. In austral spring, seal Yellow increased the percentage of time hauling out during the last week of October (week 43), while seal Red increased hauling out progressively since the end of August (week 34). For seal Red between week 42 and 47, the increment of time hauling out started at 5–6 h (10 %), with a maximum that tended to centre around solar midday and that was relatively constant (60–100 %), and then

Fig. 6 Daily overall haul out profile in relation to distance to ice edge. Maximum values of haul out match with medium-high latitudes. Minimum values are obtained when seals are far away from the pack ice



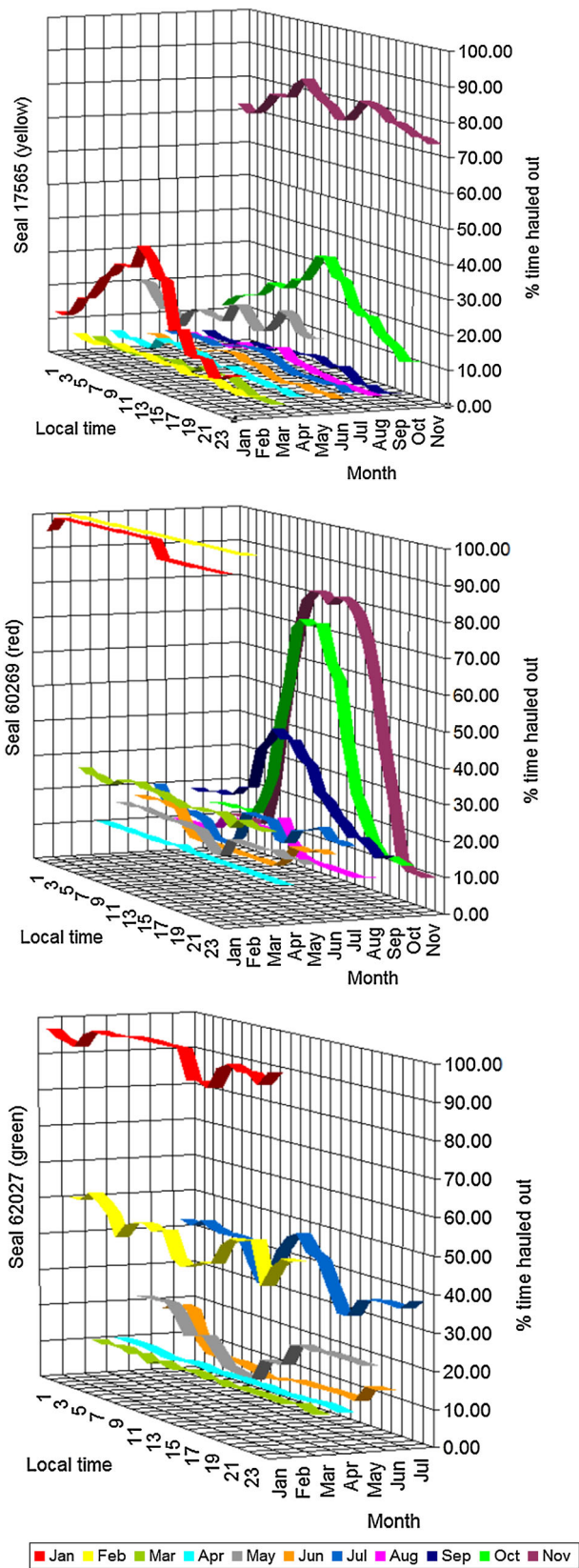


Fig. 7 Hourly haul out profiles of three Ross seals tagged with satellite transmitters for ~1 year. Each month is marked with a colour code

decreasing until 19–21 h (10 %). Thus, this increase in haul out during the day lasted between 13 and 15 h. Strikingly, seal Yellow showed a different behaviour, and at some point an inverse pattern, during the first and second weeks of November when it hauled out almost continuously. During the following 2 weeks, the seal hauled out progressively less time than in previous weeks.

Time at temperature

In January, when the seals were in high latitudes hauling out during moulting, the three seals spent most of the time (on average 37 %, range 15–51 %, *n* = 3) at a temperature higher than 4.1 °C. A similar pattern was found in November, when they (*n* = 2) hauled out at mid-latitudes for breeding with 32 % of time at a temperature higher than 4.1 °C (range 34–26 % of time). In February, when seals Yellow and Red were at the lowest latitudes, outside the Antarctic Convergence, they spent on average 49 and 43 % of time, respectively, at temperatures ranging between 1.1 and 2.0 °C. At mid-latitudes (June–October), they were exposed to a broader range of temperatures, between –1.9 and 2.0 °C, with a similar percentage of time spent in each bin (Fig. 8).

The minimum temperature (–19.9 to –10.0 °C) was registered by the transmitter on seal Red on September 25, during 8.7 h, and on 2 October, during 1.2 h, and by seal Yellow on 15 May, during 32 min. The minimum temperature for Green seal (–9.9 and –5.0 °C) was reached on 15, 16 and 18 July. This means that seals did not haul out when temperatures were really cold (<–20 °C). Most of the days (average 86.33 %, range 79.10–94.25 %) they were at a minimum between –4.9 and 0 °C. Large differences in temperature were recorded for some days, which means that the seal was both in the water and on the ice during cold days, possibly forced onto the ice to escape from a predator. The monthly overall distribution of TAT is shown in Fig. 8.

Discussion

The (limited) use of ice habitat

In this study, we tagged four adult female Ross seals in the Amundsen Sea at the late stage of moulting and tracked their movements for almost a year.

The movements of the Ross seals and the analysis of the daily distances to the ice edge confirm that the Ross seal has a truly aquatic behaviour and that it is rather an ice-associated seal than an ice-obligated species, quite independent of the heavy pack ice habitat except for moulting and breeding. The results agree with previous findings

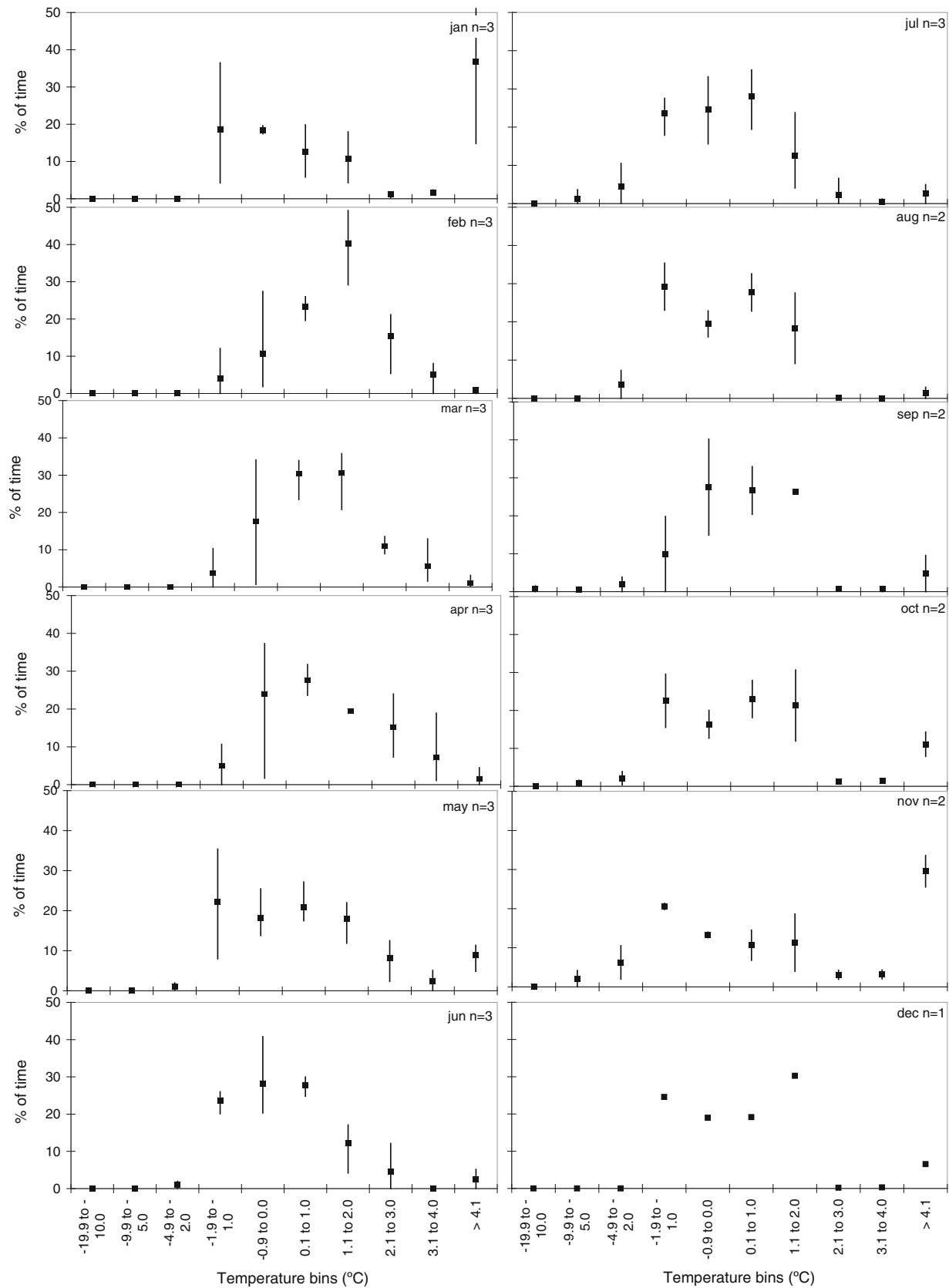


Fig. 8 Percentage of time at each temperature interval between January and December 2011 ($n =$ no. of seals). None of the three monitored seals spent TAT colder than -20°C

about the long migration Ross seals perform after moulting (Blix and Nordøy 1998, 2007; Bengtson et al. 2011). This is the reason why some authors (Kooyman and Kooyman 2009) classify Ross seals as a Sub-Antarctic seal instead of an Antarctic seal. However, since they are completely dependent on the Antarctic pack ice for moult and breeding, this seems to be more of an academic discussion, since other Sub-Antarctic seals breed on Sub-Antarctic islands.

In the present study area, the seals moved long distances from the pack ice, even out of the Antarctic Treaty System (60°S), as Blix and Nordøy (2007) also noted in King Haakon VII Sea, on the opposite side of Antarctica. This behaviour in late summer thus seems to be common in this species throughout Antarctica and refutes the old theories suggesting that Ross seals mainly inhabit the pack ice (Siniff 1991).

In the lowest latitudes, the four seals moved with comparatively low swimming speed and no persistent directionality, which may suggest that this is a foraging area (Cardona et al. 2009). The diet of Ross seals, described by Skinner and Klages (1994), consists mainly of cephalopods (47 %), but also fish (34 %) and invertebrates (19 %) including krill. Pauly et al. (1998) (quoted in Aubail 2011) estimated the trophic levels of several marine mammals mainly by stomach content analysis. Values for trophic levels ranged from 3.3 for crabeater seals (*Lobodon carcinophaga*), 4.0 for Weddell seals (*Leptonychotes weddellii*) and 4.1 for the Ross seals, suggesting that Ross seals feed on similar trophic level as the fish-eating Weddell seal.

To our knowledge, no study has been carried out on the diet when the Ross seals are in open water. Other Antarctic seals such as crabeater seals, Weddell seals and leopard seals (*Hydrurga leptonyx*) are confined to the pack ice and especially crabeater seals tend to aggregate and concentrate in the marginal ice zone, as this is where krill is more abundant during the summer bloom of plankton (Nordøy et al. 1995). During those conditions, the pelagic behaviour of the Ross seals could be an advantage, increasing foraging success and avoiding predation from leopard seals and competition from crabeater and Weddell seals. In this area, Ross seals overlap with southern elephant seals (*Mirounga leonina*), probably due to favourable foraging conditions resulting from the high eddy activity and small-scale dynamics in the Antarctic Circumpolar Current (Biuw et al. 2007).

Although the use of ice habitat is limited during large parts of the year, we have shown that the four instrumented female Ross seals in the Amundsen Sea moulted during the first part of January and that the moult occurred deep in the pack ice while the ice cover was still receding (Fig. 5). It is slightly earlier than observed by Blix and Nordøy (2007) in the King Haakon VII Sea, where the moult occurred close

to the continental shelf edge, from mid-January to mid-February, when the pack ice was at its minimum. This is consistent with the ten [five females (four ad and one subad.) and five males (four ad and one subad.)] other Ross seals that were caught from 29 December 2010 to 6 January 2011, but not tagged as their moult had just begun. The tagged adult Ross seal females therefore probably consist of the early moulters of the population.

Haul out variability depending on the individual, season and time of the day

In order to correctly estimate abundance of Antarctic seals, given its aquatic behaviour, the number of observed seals during a survey should be adjusted taking both the probability of detecting a seal on the ice and the probability that the seal was hauled out during the survey into account (Bengtson et al. 2011). In Ross seals, usually solitary individuals are found widely separated, although in a few cases they were seen in smaller groups (Bengtson and Stewart 1997; Spletstoesser et al. 2000; Thomas and Rogers 2009; Bengtson et al. 2011). The sampling probability depends on the dial pattern of haul out (Southwell 2003; Bengtson et al. 2011). Consequently, the moult period at midday has been reported to be the best time to conduct surveys (Southwell et al. 2008; Bengtson et al. 2011). However, as surveys usually occur during different times of the day, a more reliable abundance estimate can be obtained if a correction factor for particular parts of the day is applied.

In this study, we have seen that the maximum probability of haul out presents differences not only between individuals but also between weeks and time of the day (Fig. 6). This high individual variability is in line with those reported by Southwell (2003, 2008). In Southwell (2003), the maximum haul out probability of one male Ross seal was close to midday in December and early in the morning in January. No differences were found in female behaviour. In Southwell et al. (2008), the haul out behaviour of Ross seals was modelled using data from 11 SDRs deployed on adults and juveniles in several pack ice regions in the Southern Ocean. They found high daily variability in the haul out probability. For instance, on 23 December, the haul out probability ranged 19.8–69.4 % (95 % percentile ranges) and the median decreased from almost 60 % on December to 24–30 % on 10 January. Haul out percentage values used in the most recent abundance census (Fig. 7 in Bengtson et al. 2011) are about 50 % at midday. We conclude that more detailed telemetry information on dial haul out probability is needed, especially during moulting, as it is a key parameter for circumpolar abundance estimation, and of crucial importance when assessing the status of the species.

Breeding and lactation strategies of Ross seals

Little is known about breeding strategies of Ross seals and the relationship between mothers and pups. We propose that one of our tagged seals (Yellow) was giving birth and nursed the pup on the ice from 30 October to 17 November, when it was hauled out continuously. This result matches the nursing period described by Southwell et al. (2003); Blix and Nordøy (2007); Thomas et al. (1980) and, i.e. 2 weeks, in early–mid-November. This was clearly shown by three satellite-tagged females drifting on an ice floe for 14–17 days without entering the water (Blix and Nordøy 2007).

However, the other seal (Red) that still provided data during the nursing period showed a different behaviour: it entered the pack ice in early October, and until the end of November, it combined hauling out mainly during midday (Fig. 7 and Online Resource 2, week 42–47) with feeding during the rest of the day. In this area, bathymetry shows seamounts that rise more than 2,000 m, which can be associated with high productivity due to upwelling along the seamounts slope (Ackley et al. 2003). Blix and Nordøy (2007) also reported one of their four tagged females to have a similar behaviour, without hauling out and continuing its diving activity throughout the breeding period. They concluded it was a barren female because it remained deep in the pack ice together with the males.

The present study has also shown that the breeding area for Ross seals in the Amundsen Sea is located between 65 and 68°S. Both seals (Yellow and Red) resided in those latitudes during the nursing period. Tikhomirov (1975; cited in Southwell et al. 2003) reported eight pups near the Balleny Islands, with coordinates 66° 55' S and 163° 45' E, which match with our results.

We were unable to analyse the detailed nursing behaviour for seal Blue due to the lack of haul out information, and for seal Green, as the transmitter stopped in July. However, seal Blue was present in the breeding area when the transmitter stopped.

This study shows the first data on temperature preference and how temperature affects the haul out behaviour of Ross seals. The majority of the time seals stayed at temperatures between -2 and $+2$ °C. Given the limited time hauled out during most months, this must be considered the temperature range of the water. Evidently, the seals did not haul out when temperatures drop below -5 °C during any time of year except for very brief periods. Even the interval -2 to -5 °C was only used a few per cent of their time during July–November. It is clear that during the months with significant haul out time, January, May and September–November, approximately 10–30 % of their time was spent at temperatures above 4 °C, which can be considered the preferred temperatures for hauling out.

The reason why the monitored Ross seals in this study hauled out for only 1 day on approximately the same date in May (16, 17 and 21 May), after having travelled a huge distance (5,245 km seal Yellow, 4,001 km seal Blue, 4,582 km seal Red and 2,306 km seal Green) is still a mystery.

Because of the limited use by Ross seals of the ice habitat (except for moulting and breeding), we suggest they may be less vulnerable than other Antarctic seals to ice recession due to climate warming.

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