

# Deep into the ice: over-wintering and habitat selection in male Atlantic walruses

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**ABSTRACT:** New technological developments in animal-borne satellite-tracking devices in combination with increased access to satellite-based environmental data are creating new possibilities for studying movement patterns and habitat selection by animals in remote, logistically challenging environments. In the present study, we report the first year-round data on movement patterns of walruses in the High Arctic, including at-sea positions. Using first-passage times (FPT) to study habitat use and quantifying habitat selection using mixed-effects Cox proportional hazards models, we dispelled the conventional perception that seasonal movement patterns of Atlantic walruses are simply a result of them following the retraction and expansion of annually formed sea ice. Walruses in this study ( $n = 17$  males) actively moved into areas of high ice concentration (>90%) during winter; travelling far into the ice pack, as far as 600 km from ice-free water. Additionally, high inter-annual, seasonal site fidelity was documented. Seasonal differences in habitat use patterns were also observed. In summer, when walruses feed intensively, FPTs were affected by water depth and distance to the coast ( $R^2 = 0.571$ ), but these variables had no effect on walrus habitat use in winter. Sea ice concentration was the most important environmental condition during the winter season ( $R^2 = 0.162$ ), though there are clearly other factors influencing where individuals occur in winter that are currently unaccounted for in these analyses. The male walruses in this study did not do much benthic diving during winter, suggesting that they did not feed often during the time that they are known to breed. Instead, they remained in areas with high ice coverage, far from their coastal summering areas, spending much of their time hauled out or in surface waters.

**KEY WORDS:** Cox proportional hazards models · First-passage time · *Odobenus rosmarus rosmarus* · Random-effects models · Satellite telemetry · Site fidelity

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## INTRODUCTION

The study of movement patterns and habitat selection has been a fundamental component of animal ecology for many decades (e.g. Manly et al. 2002, Fortin & Dale 2005). But, in marine mammal research, this field has progressed slowly compared to terrestrial studies because of the technological problems encountered in attempting to track animals at sea (Cooke et al. 2004). New tag technology (e.g. Fedak et al. 2002,

McConnell et al. 2004, Robinson et al. 2006), in combination with greater access to satellite-based and other environmental data, as well as new statistical approaches to the study of animal movements in relation to environmental correlates (e.g. Aarts et al. 2008, Freitas et al. 2008b), are opening up new possibilities for studying animals even in remote, very logistically challenging environments. Extensive sea ice, harsh weather and sea conditions, in addition to 24 h winter darkness has limited our ability to work with large,

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highly mobile Arctic marine mammals, leaving winter ecology and habitat use largely enigmatic for many species. The new possibilities to study these 'problematic' animals and the environmental conditions they experience by using remote methods are very timely, because the Arctic is currently undergoing dramatic environmental change (ACIA 2005, Solomon et al. 2007). Monitoring a resident population's responses will provide considerable insight into their adaptability and permit assessments of their survival potential.

Walrus *Odobenus rosmarus* are full-time residents of the Arctic. Our current knowledge of their movement patterns and habitat selection choices is a composite built from bits of information from many, different sources, including aboriginal hunting knowledge and catch records (e.g. Lønø 1972, Fay 1982, Fay et al. 1984), natural history observations, some of which date back to early Arctic explorers (e.g. Allen 1880 and references therein, Manning 1944, Mansfield 1958, 1966), military flights and naval operations (e.g. Fay 1982), inferences from isotope patterns in teeth (Stewart et al. 2003), as well as some dedicated studies of behaviour and demographics (e.g. Miller 1982, Miller & Boness 1983, Born & Knutsen 1992, 1997, Knutsen 1993, Gjertzt & Wiig 1995, Sjare & Stirling 1996, Wiig et al. 1996, Gjertzt et al. 2001, Jay & Hills 2005, Lydersen et al. 2008). Not surprisingly, most of the available behavioural information about walrus is restricted to the seasons in which there is daylight in the High Arctic (i.e. not in the winter). Some data are available from both walrus subspecies (Atlantic: *O. r. rosmarus*; Pacific: *O. r. divergens*), but our general picture of walrus ecology is often dominated by Fay's (1982) monograph on the Pacific walrus.

During summer, male walrus occur mainly in seasonally ice-free coastal, shallow water (80 to 100 m deep) areas, where they feed on bottom-dwelling bivalve molluscs, hauling-out on land intermittently to rest (Fay 1982, Gjertzt & Wiig 1992, Wiig et al. 1993, Fisher & Stewart 1997, Gjertzt et al. 2001, Born et al. 2003). Females and calves seem to prefer to remain in association with drifting ice as much as is possible, but they too occur in coastal areas in summer throughout the range of the species (Fay 1982, Miller 1982, Miller & Boness 1983, Gjertzt & Wiig 1994). The reproductive status of hunted specimens and the single observational study of mating behaviour conducted to date indicate that mating takes place from January to April (Mansfield 1966, Fay 1982, Fay et al. 1984, Sjare & Stirling 1996, Born 2001, 2003). Breeding locations for most walrus populations are unknown. However, during the winter and early spring, male and female walrus in the Pacific are found mainly in pack-ice areas close to ice edges (Fay 1982, Fay et al. 1984). It is believed that Pacific walrus follow the seasonal

advance and retreat of sea ice throughout the year, migrating south in winter and north in summer (Fay 1982, 1985). The same pattern has been assumed to occur for Atlantic walrus, though little movement information is in fact available. Locally, in the eastern Canadian Arctic and West Greenland, distribution is thought to be governed by bathymetry, ice conditions and the influence of native settlements (Born et al. 1995).

Studying movement patterns and habitat selection directly via the deployment of satellite-linked tags on walrus has proven to be very challenging. These large animals are not easily anaesthetised, and they are very rough on instruments. Previous telemetry studies have been attempted in both Atlantic (Born & Knutsen 1992, 1997, Wiig et al. 1996, Born et al. 2005, Born & Acquarone 2007) and Pacific walrus (Jay & Hills 2005). However, the durations of data records have not been long enough to reveal breeding locations in most cases, at-sea position data have not been received by the satellite platform and relatively little habitat analysis has been conducted.

Atlantic walrus in Svalbard (Norway) and Franz Josef Land (FJL; Russia) belong to a single population (Born et al. 1995, Andersen et al. 1998). In these High Arctic archipelagos, 4 centuries of harvesting severely depleted the walrus population, especially in Svalbard (Lønø 1972, Born 1984, Born et al. 1995, Gjertzt & Wiig 1995). Recovery has been taking place since walrus became protected during the early 1950s (Born 1984, Gjertzt & Wiig 1995). Currently, the summering population in Svalbard is estimated to be approximately 2600 individuals (Lydersen et al. 2008). Walrus found along the coasts of Svalbard are predominantly males (Gjertzt & Wiig 1994); females are rarely observed beyond a small area in the far NE corner of the archipelago (Gjertzt & Wiig 1994). Females and calves are, however, common in FJL (Knutsen 1993, Gjertzt & Wiig 1994). Although walrus in Svalbard and FJL form a single population, and movements between the 2 archipelagos have been reported during summer and autumn (Wiig et al. 1996), it is not known if male walrus from Svalbard travel to FJL in winter/spring to mate. It is possible that females from FJL migrate south in winter, as they are purported to do in the Pacific, and that mating areas occur south of that archipelago.

In the present study, annual movements and habitat selection by male walrus tagged in Svalbard in the summers of 2003 and 2004 were investigated, with special emphasis on their movement patterns and habitat-use during winter. Based on male movements during that time of the year, breeding locations and the duration of breeding were also investigated. Fidelity to feeding and breeding areas between years was also explored.

## MATERIALS AND METHODS

**Field methods and data handling.** A total of 17 male walrus were equipped with custom-designed, satellite-relayed data loggers (SRDL) in August 2003 ( $n = 9$ ) and August 2004 ( $n = 8$ ) in Svalbard, Norway (Table 1, Fig. 1). The SRDLs were designed to give information on the movements (geographic position), haulout time and diving behaviour (depth) of the walrus (see Lydersen et al. 2008 for design details, SRDLs produced by SMRU, St. Andrews University). Animal handling procedures followed Griffiths et al. (1993), with the methodological modifications described by Lydersen et al. (2008). All animal-handling protocols used in this study were approved by the Governor of Svalbard (Sysselmannen) and the Norwegian Animal Research Authority. A SRDL was attached to the left tusk of the immobilised individual using stainless steel hose clamps. Tusk length and circumference at the base were measured ( $\pm 1$  cm); tusk volume (or mass) increases continually with age in walrus and, hence, provides a crude estimator of age (Fay 1982). Volume ( $V$ ) was calculated assuming that tusks were cone-shaped, using the relationship:

$$V = \frac{1}{3} \pi r^2 h$$

where  $r$  is tusk radius and  $h$  is the length of the tusk.

The SRDLs provided position, dive and haulout data. These data were received through the Advanced

Research and Global Observation Satellite (ARGOS) system of geosynchronous satellites. The SRDLs were programmed to send these data whenever possible, with a transmission rate of up to 250 transmissions  $d^{-1}$  during the first 100 d and 140 transmissions  $d^{-1}$  thereafter. ARGOS locations are estimated by Doppler shift (not by GPS). Because of the high number of low-accuracy locations, ARGOS locations were filtered using the algorithm described by Freitas et al. (2008c) and available within the R software package 'argosfilter' (<http://cran.r-project.org/>; function `sdafilter` with all default settings). Filtering aimed to remove locations requiring unrealistic swimming speeds ( $>2$  m  $s^{-1}$ ) and unlikely turning angles ( $>165$  degrees or  $>155$  degrees, depending on the length of path deviations). Quality 'Z' locations (for which the location assessment process failed; see ARGOS 1996) were also removed.

**Movement parameters and home range analysis.** Distances travelled and travelling speeds were calculated using ArcInfo (ESRI, Inc.). In order to investigate home range size and site fidelity throughout the year, home ranges were calculated for each month for each walrus, using the 100% minimum convex polygon (MCP) method (Mohr 1947). This simple method was chosen since it provides the limits of the overall area used by each individual, which was the focus of interest in the present analysis. First and last months in the data sets were excluded from this analysis if they did not contain a minimum of 20 d of data. Calculations were made using the package 'adehabitat' in R. The

Table 1. *Odobenus rosmarus*. Summary of tracking records and tusk measurements of 17 adult male walrus equipped with satellite-relayed data loggers in Svalbard in 2003 and 2004. Seasons tracked —S: summer; W: winter. Wintering area—SS: south Svalbard; WS: west Svalbard; NES: northeast Svalbard; K: Kvitøya; FJL: Franz Josef Land; \*same as the tagging area; \*\*travelled to FJL in summer, did not concentrate time in any particular area during winter

Walrus ID	First location	Last location	No. days tracked	No. raw locations	No. filtered locations	Seasons tracked	Wintering area	Tusk length (cm)	Tusk perimeter (cm)	Tusk volume (cm <sup>3</sup> )
2003_01	6 Aug 2003	30 Mar 2004	237	1110	765	S/W	SS*	42	19	402
2003_02	6 Aug 2003	5 May 2004	273	1197	760	S/W	SS*	34	19	326
2003_03	6 Aug 2003	22 Oct 2004	443	2240	1483	S/W/S	FJL	53	24	810
2003_04	6 Aug 2003	24 Mar 2004	231	1182	846	S/W	-**	37	20	393
2003_05	6 Aug 2003	14 Feb 2004	192	1112	512	S/W	K	43	22	552
2003_06	6 Aug 2003	23 Mar 2004	230	1395	875	S/W	FJL	39	23	547
2003_07	6 Aug 2003	30 Oct 2004	451	1667	1046	S/W/S	NES	45	17	345
2003_08	5 Aug 2003	4 Mar 2004	212	1319	809	S/W	WS	45	19	431
2003_09	6 Aug 2003	5 Nov 2004	457	2133	1481	S/W/S	K	46	17	353
2004_01	5 Aug 2004	29 Jan 2005	177	378	239	S/W	NES	-	24	-
2004_02	5 Aug 2004	16 Dec 2004	133	563	294	S/W	NES	43	19	412
2004_03	4 Aug 2004	7 Oct 2004	64	497	353	S	-	-	-	-
2004_04	5 Aug 2004	12 Mar 2005	219	793	585	S/W	K	40	22	514
2004_05	5 Aug 2004	31 Mar 2005	238	1962	1229	S/W	K	37	21	433
2004_06	4 Aug 2004	17 Sep 2005	409	1007	720	S/W/S	NES	48	30	1146
2004_07	4 Aug 2004	25 Feb 2005	205	221	163	S/W	NES	50	19	479
2004_08	5 Aug 2004	6 Feb 2006	550	1529	1035	S/W/S/W	K	43	20	456
Mean				278						
SE				32.4						

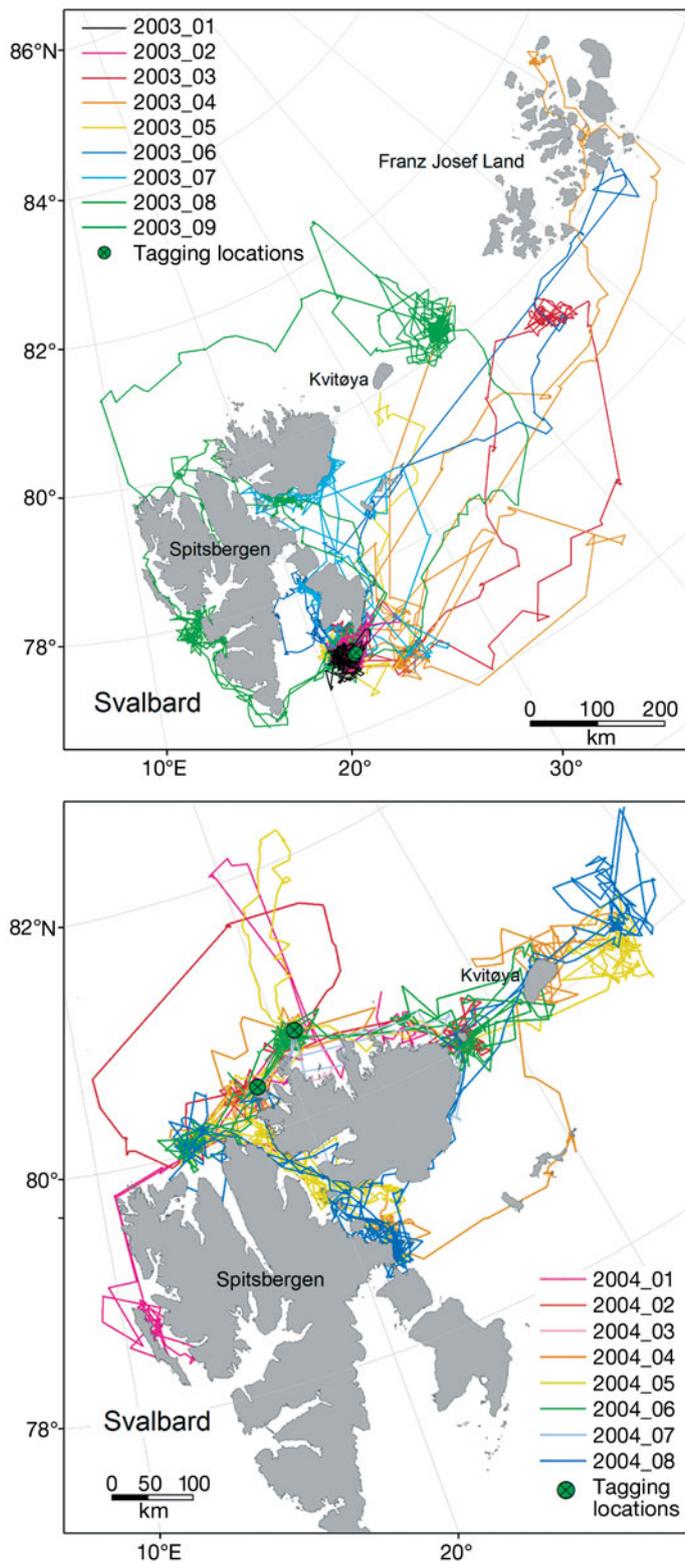


Fig. 1. *Odobenus rosmarus*. Tracks of 17 male walrus equipped with satellite-relayed data loggers in Svalbard in 2003 (upper panel) and 2004 (lower panel), filtered following the method described by Freitas et al. (2008c)

percentage overlap between home ranges was calculated, using the R package 'spatstat'.

**Habitat selection analysis.** Using the filtered locations and assuming that walrus travelled linearly at constant speed between those locations, a set of positions was generated every 10 km along the track of each individual. This resolution (10 km) was chosen in order to have a resolution equal to, or lower than, the resolution of the environmental variables used to explore habitat selection (see below). Filtered locations were spaced at median ( $\pm$ SE) distances of  $3.0 \pm 0.1$  km, and thus had a finer resolution than the generated positions. First-passage times (FPT) were then calculated for each of the generated positions, in order to obtain a measure of habitat use intensity along the track. FPT is defined as the time required for a tracked animal to cross a circle of a given radius (see Fauchald & Tveraa 2003). FPTs were calculated for every position for radii ranging from 10 to 100 km (by 10 km increments). The variances of the log-transformed FPTs were then plotted for each individual in order to identify the radius of maximum variance. This radius corresponds to the spatial scale at which the animal concentrated its time and, hence, is the scale that best differentiates between high and low passage times (Fauchald & Tveraa 2003, 2006). The scale of maximum variance (mean scale for all study individuals) was found to be 40 km (Fig. 2). FPTs at this scale were used to compare the time spent by walrus in different parts of their tracks. Note that a common scale was used to make inter-individual comparisons possible.

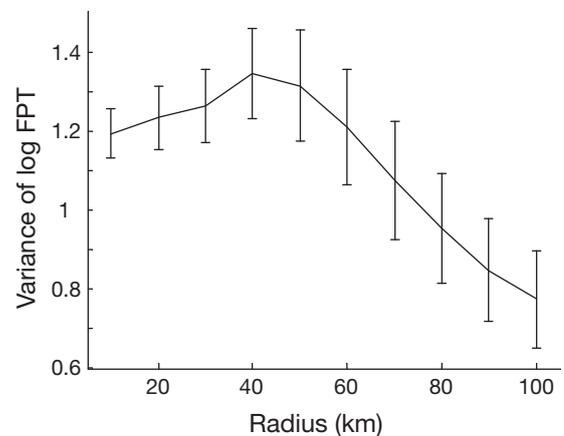


Fig. 2. *Odobenus rosmarus*. Mean variance ( $\pm$ SE) in log-transformed first-passage times (FPT) as a function of radius for the 17 male walrus tagged in Svalbard in 2003 and 2004. The peak in variance occurred at a radius of 40 km

In order to explore the hypothesis that habitat selection during the breeding (winter) and feeding (summer) seasons were driven by different environmental conditions, FPTs were analysed separately for these 2 seasons. Atlantic walrus breed during winter and spring, mainly between January and April (Mansfield 1966, Sjare & Stirling 1996, Born 2001, 2003); males feed little during that season, but feed intensively during summer (Fay 1982). In order to identify possible

breeding areas (where walrus had high FPTs), walrus locations in each track were colour-coded to aid visualization, according to the FPTs at a 40 km radius. Areas where walrus concentrated their time during winter/early spring were categorised as breeding areas (see Fig. 3). All other locations, except movements to/from breeding areas were categorised as feeding areas. To further explore the use of wintering and summering areas, diving behaviour of these ben-

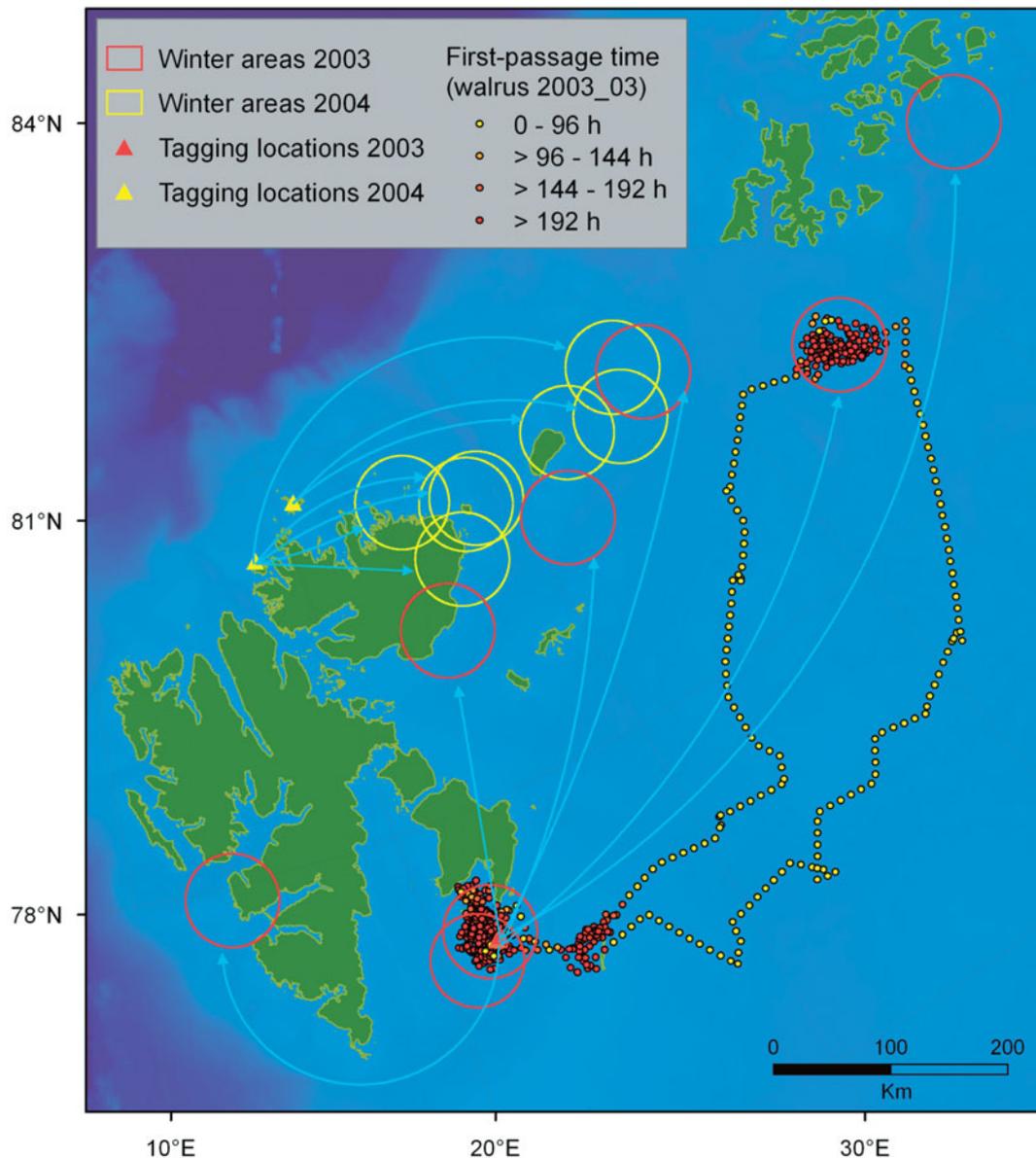


Fig. 3. *Odobenus rosmarus*. Areas where walrus tracked in this study concentrated their time during the winter/breeding season (circles). Note that one walrus was not tracked during winter (walrus 2004\_03), and another did not concentrate its time in any particular area during winter (2003\_04); therefore only 15 wintering/breeding areas are shown. Walrus were tagged in Svalbard in 2003 and 2004, in the locations indicated by the triangles. The detailed track information for 1 walrus (2003\_03) (10 km spaced positions) is presented as an example of an actual track. It is colour-coded according to first-passage time (FPT, 40 km radius); colours range from yellow (low FPTs) to red (high FPTs)

thic feeders was investigated in a preliminary fashion, comparing maximum depth of each dive with bathymetry in areas of high usage on a seasonal basis (detailed analyses of diving behaviour will be published separately). Sea bottom depths were extracted from 2.5 km resolution grid data from IBCAO (International Bathymetric Chart of the Arctic Ocean, Version 1.0, 2001). Note that all dives performed by the tracked animals are recorded by the SRDLs, but not all of them are received through the ARGOS system (because of satellite availability or transmission interruptions when the antenna is submerged). In this study dive information was available for  $76.0 \pm 4.4\%$  of the tracking time (mean  $\pm$  SE,  $n = 17$  walruses), with a total of 109 741 dives being received during the entire tracking time).

In order to investigate habitat conditions associated with walrus habitat utilization (walrus FPTs) in breeding and non-breeding areas, a set of environmental conditions that could potentially affect FPTs were obtained for the same positions where FPTs were calculated. The variables included were: sea ice concentration (percent of water covered by sea ice), water depth, distance to the coast and distance to the nearest glacier front. The latter variable was included because coastal glacier fronts are known to attract other Arctic marine mammals because of the high levels of productivity generated in these areas (e.g. Lydersen et al. 2001, Freitas et al. 2008a). It is highly likely that sea-bottom sediment type also affects habitat use by these benthic feeders, but such data are not available for the study area. Sea ice concentrations were obtained from daily 10 km resolution data from OSI-SAF (The Ocean and Sea Ice Satellite Application Facility), which are derived from NASA SSM/I data. Depths were extracted from 2.5 km resolution grid data from IBCAO. Distances to the coast and to the nearest glacier front were calculated from Norwegian Polar Institute digital maps (updated using aerial photographs of glacier fronts and coastlines taken from 1993 to 1998).

The effect of habitat attributes on FPTs was first investigated by plotting the bootstrapped 95% confidence intervals (CIs) of FPTs as a function of the variable of interest. CIs were obtained using the percentile method (with 5000 bootstrapping samples). The effect of all habitat conditions on FPTs was then investigated by modelling FPTs, as a function of these variables, using Cox proportional hazard models (CPH models; Cox 1972). A detailed description of this method was presented by Freitas et al. (2008b) The CPH model is written as:

$$h(t) = \exp(\beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \dots + \beta_p X_p) h_0(t)$$

where  $h(t)$  is the hazard function, i.e. the risk of an animal leaving an area at time  $t$ .  $X_1, X_2, X_3, \dots, X_p$  are the

explanatory variables in the model, and  $\beta_1, \beta_2, \beta_3, \dots, \beta_p$  are the coefficients that describe the contribution of these variables.  $h_0(t)$  is the baseline hazard function at time  $t$ , i.e. the risk of leaving an area where all explanatory variables are equal to zero or to a defined base value. In order to take individual variability into account, a random-effect term ( $b$ ) was added to the general CPH model, as described by Pankratz et al. (2005):

$$h(t) = \exp(\beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \dots + \beta_p X_p + b) h_0(t)$$

where  $b$  is the per-subject random effect. This modification of the general CPH model allows for analysis of time-based event data that have a nested variance structure.

Selection of the best model was based on the Akaike's information criterion, corrected to the effective sample size ( $AIC_c$ ; Burnham & Anderson 2002). All possible combinations of variables were considered during model selection. The key assumption of proportional hazards required by the CPH model was tested by checking the scaled Schoenfeld residuals, both visually and by testing if their slope was zero (see Collett 2003). The variable 'distance to glacier' was evaluated by the bootstrap procedure explained above, which showed that it had no clear effect on habitat selection. In addition this variable did not fulfil the proportional hazards assumption and was therefore excluded from further analyses. All other variables included in the analysis fulfilled the required proportional hazards assumption. FPT modelling was performed in R (packages 'survival' and 'kinship').

The models were fitted separately for non-breeding and breeding areas. Movements between feeding and breeding areas were considered to be breeding movements and were hence analysed together with the breeding locations. Since non-breeding areas (summering areas) were generally located close to the coast and sea ice concentrations were not available in such areas, due to the land-masking process, sea ice concentration was not included as a covariate when modelling FPTs in these areas. Note that there was in fact little sea ice in coastal waters during the summers within the study period; the sea ice edge was located well north of the summering areas of the tracked walruses.

Summary statistics are hereafter presented as means  $\pm$  SE or as median values (with first and third quartile values). Since the number of locations varied between individuals (see Table 1), mean values obtained from data pooled across individuals are presented as the mean of the mean values of each individual. The same was done for the medians.

## RESULTS

### Movements, over-wintering and site fidelity

Movement data for individual walrus were obtained for periods ranging from 2 to 18 mo and included either part of, or the complete, breeding season for 16 of 17 individuals (Table 1). During summer, walrus were most often found in coastal areas; median distance to the coast was 4.6 km (3.7 to 5.6 km). Monthly home ranges varied greatly between individuals (182 to 91 113 km<sup>2</sup>). Large summer home ranges were mainly obtained from individuals moving along the coasts of Svalbard. Only 1 walrus performed an offshore trip (to FJL) during summer (walrus 2003\_04; Fig. 1).

During winter, most walrus performed long-distance movements, reaching areas up to 840 km from the tagging locations (Figs. 1 & 3). They travelled up to 670 km (linear distance) in 10 d. When they reached specific areas (assumed to be breeding areas), they occupied them for 20 to 226 d (Fig. 4); the mean period was  $120 \pm 24$  d for the individuals with known returning dates. Walrus performed offshore winter movements between early October and early February and returned between late February and late June (Fig. 4). During these trips, the walrus did not follow the ice edge as the sea ice advanced or retreated. Instead, they moved far into areas with increasing ice coverage, using areas as far as 600 km from ice-free areas, with

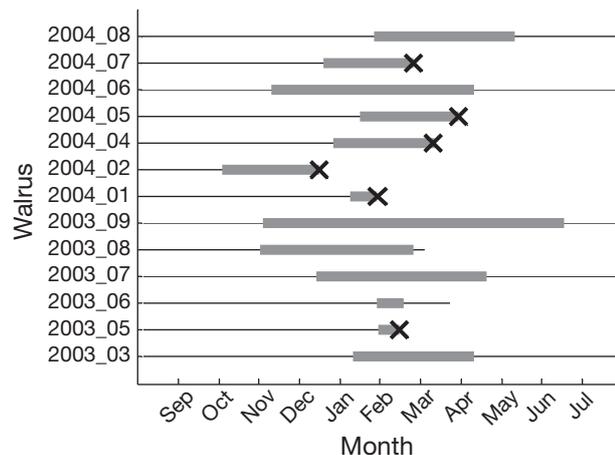


Fig. 4. *Odobenus rosmarus*. Time spent at the wintering/breeding areas by male walrus tagged in Svalbard in 2003 and 2004 (thick lines). Thin lines indicate duration of the tracking records. Contact with some walrus was lost during the breeding season as indicated by the symbol **x**. Tick marks on the x-axis correspond to the first day of each month. Note that 4 walrus are not shown in the figure since they did not move to any particular breeding area during winter (2003\_01, 2003\_02 and 2003\_04; see Figs. 1 & 3) or there were no data available from winter (2004\_03)

ice concentrations as high as 100 % (Fig. 5). Median sea ice coverage encountered along the paths of these trips was 84.5 % (64.3 to 89.4 %; values calculated from locations at 6 h intervals along the tracks). The winter destinations of walrus were linked to their summer locations. Individuals tagged at 2 sites in the north of Svalbard, that were still sending data in winter ( $n = 7$ ) performed relatively short winter trips, travelling only to the NE corner Svalbard ( $n = 4$ ) or just to the east of Kvitøya (Figs. 1 & 2, Table 1). Winter movements of walrus tagged in the southeast of Svalbard ( $n = 9$ ) were more variable. Most of these males moved towards the northeast; 1 only went as far as the NE corner of Svalbard, 2 stopped just south and east of Kvitøya, while 2 others went as far as FJL (Figs. 1 & 3, Table 1). Three individuals did not move toward the NE; 1 of these (walrus 2003\_08) moved a significant distance coastally, going around the southern point of Spitsbergen to the west coast, while the other 2 (walrus 2003\_01 and 2003\_02) remained in their summer locations (Figs. 1 & 3, Table 1). The 2 walrus that did not travel in winter, as well as walrus 2003\_04, which did travel offshore, but during summer, were probably relatively young, based on their tusk volumes (Table 1).

After the breeding season, all of the walrus still sending locations ( $n = 5$ ) showed fidelity to the previous year's summering areas, with home range overlaps were as high as 71 % for the month of August (mean overlap was  $35.0 \pm 12.7$  %; see Fig. 6). Only 1 individual was tracked for a long enough period for positions to be obtained during a second winter (walrus 2004\_08), and this tag only provided 2 locations during the second breeding season. But, both of these locations overlapped the MCP area used in the previous breeding season, located NE of Svalbard (see Fig. 1).

### Habitat selection

The rankings of alternative CPH models for non-breeding and breeding areas are shown in Tables 2 & 3, respectively. During the non-breeding season, FPTs at the radius of 40 km varied dramatically, ranging from 13 h to 189 d (mean:  $31.7 \pm 6.2$  d). Areas of intense usage (high FPTs) occurred in shallow areas, close to the coast, as indicated by the bootstrapping confidence intervals (Fig. 7). The same pattern was obtained both when including or excluding the time spent hauled out. Accordingly, higher risk of leaving an area was found with increasing depths (>40 m) and at increased distance from the shore (Table 4). For example, the risk of leaving an area was 2.6 times higher in waters deeper than 80 m compared to areas shallower than 20 m (see hazard ratios in Table 4). In areas located at >60 km from the coast, the risk of leaving was approxi-

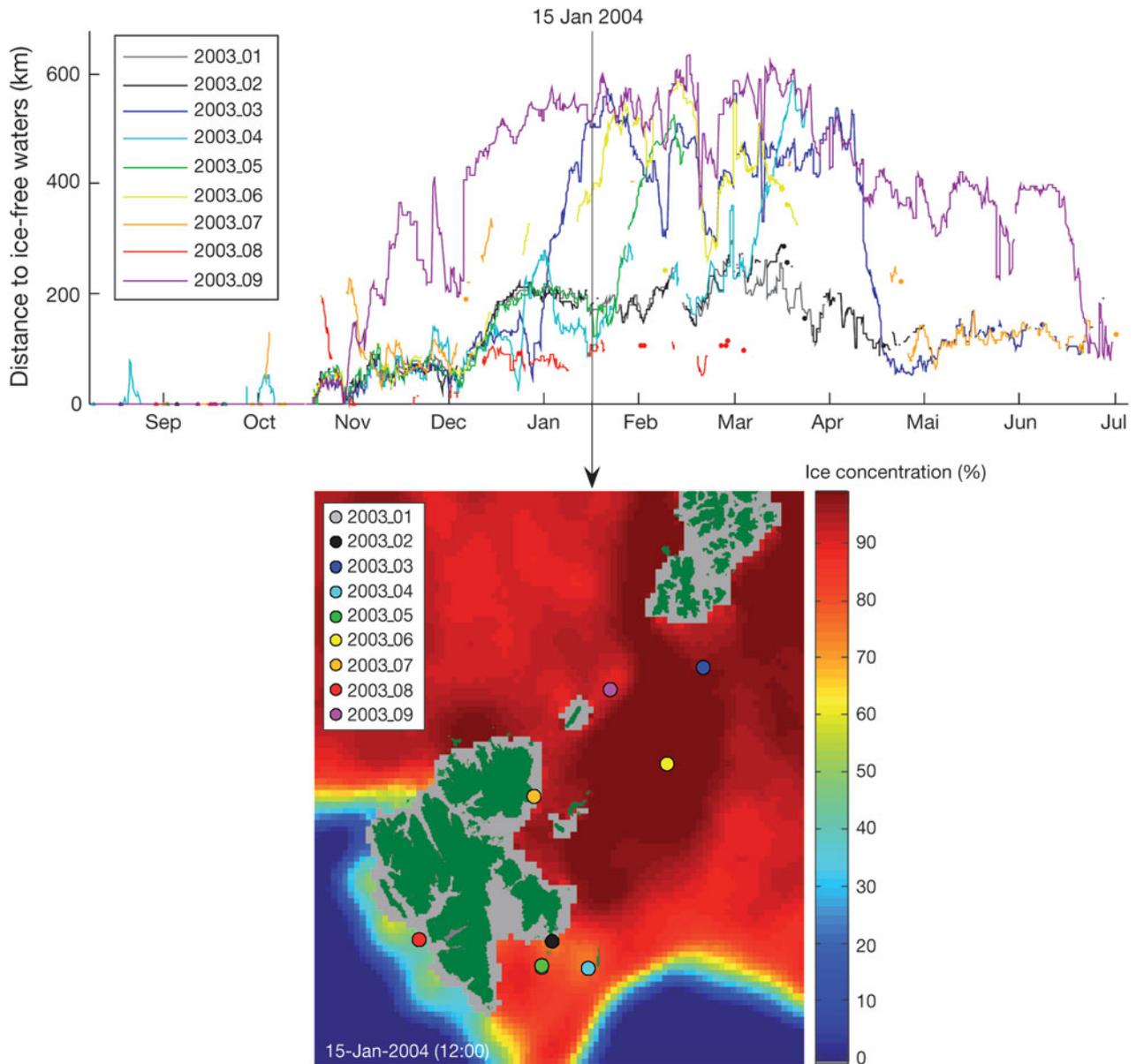


Fig. 5. *Odobenus rosmarus*. Distances to ice-free areas throughout the year for walruses tagged in Svalbard in August 2003 (upper panel). Tick marks on the x-axis correspond to the beginning (first day) of each month. Lower panel gives the location of the walruses on 15 January 2004, a day selected during the peak period of ice cover. Note that the locations of walruses 2003\_01 and 2003\_05 overlap. Sea ice concentrations in the lower panel range from 0 to 100%. No ice information is available for the coastal areas shown in grey

mately 9 times higher than in areas up to 20 km from the coast. These 2 variables explained 57.1% of the variability in the data (Table 2). The variance component attributed to individual variability was 0.627. The standard deviation of the per-individual random effects ( $\sqrt{0.627} \approx 0.792$ ) indicates that the average spread of relative risk of leaving among individuals was  $e^{0.792} \approx 2.21$ , meaning that the per-individual variability in the probability of leaving was on average 2.2 times higher or smaller than the overall probability.

When using wintering/breeding areas, or when in transit to those areas, FPTs at the spatial scale of 40 km radius ranged from 20 h to 82 d (mean:  $19.3 \pm 3.6$  d). Mean water depth used in these areas was  $125 \pm 18.7$  m. Neither the bathymetry nor the proximity to a coastline affected FPTs during the winter season (see Tables 3 & 5). Note that water depth was included in the most parsimonious model, but its effect on FPTs was not significant (see confidence intervals in Table 5). Higher risks of leaving were observed at the

beginning and end of the breeding season (October and June), reflecting the transit to and from the breeding areas. Lower risks of leaving were also observed in ice-covered waters, but sea ice concentration and

month together explained only 29.0% of the variability in the FPT data (Table 3). The variance component attributable to individual variability in the wintering/breeding areas was 1.45.

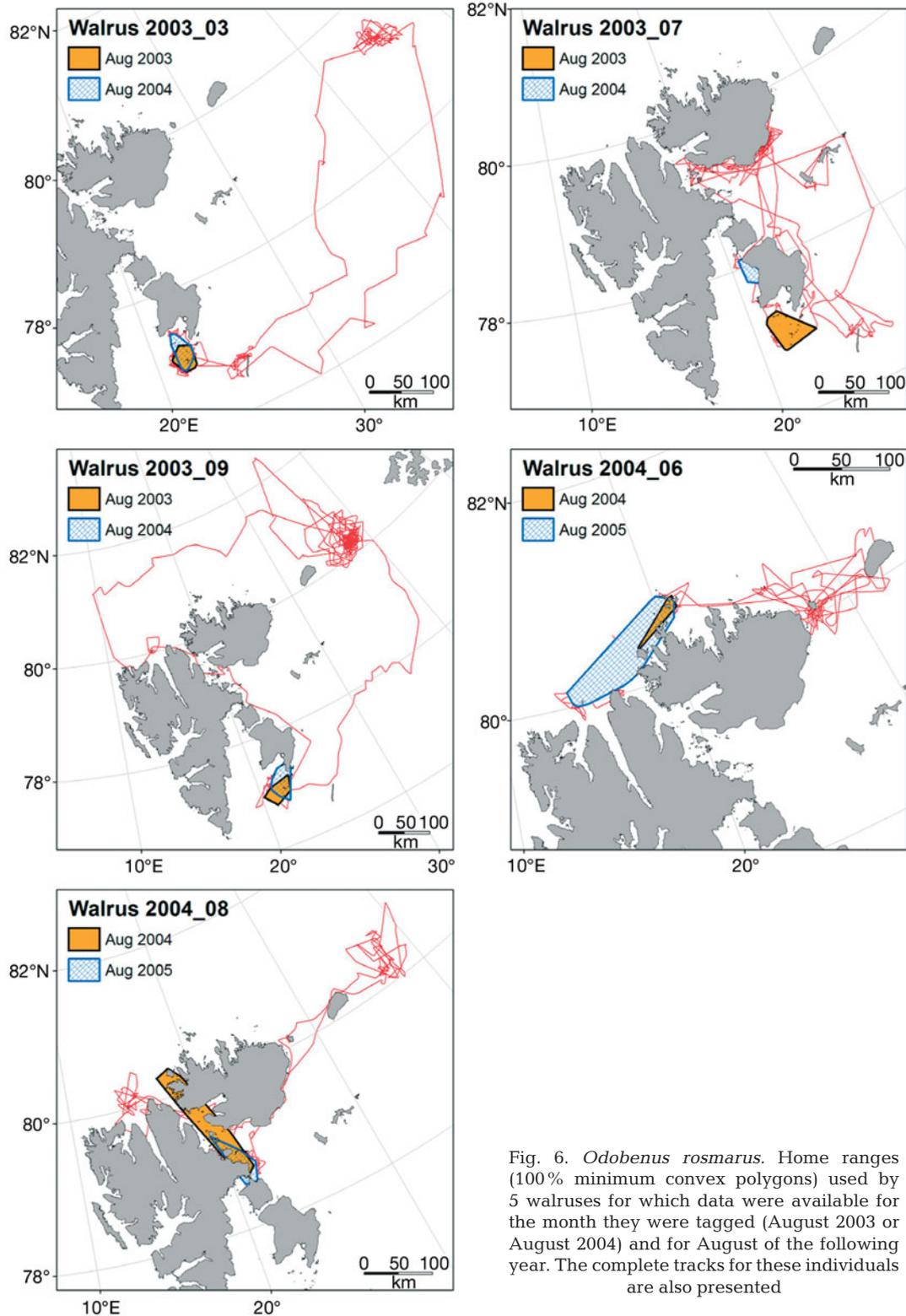


Fig. 6. *Odobenus rosmarus*. Home ranges (100% minimum convex polygons) used by 5 walrus for which data were available for the month they were tagged (August 2003 or August 2004) and for August of the following year. The complete tracks for these individuals are also presented

Table 2. *Odobenus rosmarus*. Model ranking (most parsimonious model at the top) for summer/non-breeding areas for walrus in Svalbard based on Akaike's information criteria corrected to the actual sample size ( $AIC_c$ ).  $AIC_c$  differences ( $\Delta_i$ ), Akaike weights ( $w_i$ ) and coefficients of determination ( $R^2$ ) are also presented, together with the penalised log-likelihoods ( $\log(L)$ ) and penalised degrees of freedom (df) used to calculate the  $AIC_c$  values. Sample size is 1564. Depth: sea bottom depth (4 categories: 0–20 m, >20–40 m, >40–60 m and >60 m); Coast: distance to the coast (4 categories: 0–20 km, >20–40 km, >40–60 km and >60 km)

Model	$AIC_c$	$\Delta_i$	$w_i$	$R^2$	$\log(L)$	df
Depth + Coast	18 611.6	0	1.00	0.571	-9 283	22.6
Depth	18 726.3	114.7	0.00	0.535	-9 344	18.6
Coast	18 786.3	174.7	0.00	0.518	-9 373	19.6

Table 3. *Odobenus rosmarus*. Model ranking (most parsimonious model at the top) for breeding areas for walrus tagged in Svalbard based on the Akaike's information criteria corrected to the actual sample size ( $AIC_c$ ).  $AIC_c$  differences ( $\Delta_i$ ), Akaike weights ( $w_i$ ) and coefficients of determination ( $R^2$ ) are also presented, together with the penalised log-likelihoods ( $\log(L)$ ) and penalised degrees of freedom (df) used to calculate the  $AIC_c$  values. Sample size is 634. Conc: sea ice concentration (6 categories: 0%, >0–20%, >20–40%, >40–60%, >60–80% and >80–100%); Month: calendar month (9 categories: Jan, Feb, Mar, Apr, May, Jun, Oct, Nov and Dec); Depth: sea bottom depth (4 categories: 0–20 m, >20–40 m, >40–60 m and >60 m); Coast: distance to the coast (4 categories: 0–20 km, >20–40 km, >40–60 km and >60 km)

Model	$AIC_c$	$\Delta_i$	$w_i$	$R^2$	$\log(L)$	df
Conc + Month + Depth	4381.9	0	0.64	0.334	-2164	26.14
Conc + Month + Depth + Coast	4383.0	1.1	0.36	0.339	-2163	28.18
Conc + Month	4402.7	20.8	0.00	0.290	-2179	22.26
Conc + Month + Coast	4405.8	23.9	0.00	0.291	-2178	24.23
Conc + Depth	4434.7	52.8	0.00	0.218	-2200	17.30
Conc + Depth + Coast	4434.9	53.0	0.00	0.226	-2198	19.53
Conc	4458.2	76.3	0.00	0.162	-2215	13.73
Conc + Coast	4460.8	78.9	0.00	0.165	-2215	15.72
Month + Depth + Coast	6775.9	2394.0	0.00	0.267	-3362	25.04
Month	6804.1	2422.2	0.00	0.218	-3383	19.06
Depth + Coast	6823.5	2441.5	0.00	0.188	-3395	16.64
Depth	6834.7	2452.8	0.00	0.166	-3403	14.08
Coast	6847.0	2465.1	0.00	0.146	-3411	12.84

Table 4. *Odobenus rosmarus*. Estimated coefficients ( $\beta$ ), hazard ratios ( $e^\beta$ ) and 95 % confidence intervals ( $CI(\beta)$ ) of the mixed-effects Cox proportional hazards (CPH) model for the covariates affecting the risk of leaving a non-breeding area by male walrus in Svalbard. Numbers of locations in each category are also given (n). Note: A  $\beta$ -value  $>0$  ( $e^\beta > 1$ ) indicates an increased risk of leaving, while a  $\beta$ -value  $<0$  ( $e^\beta < 1$ ) is interpreted in the opposite way

Variable	n	$\beta$	$e^\beta$	$CI(\beta)$
Depth ( $\leq 20$ m)	478	–	–	–
Depth (>20–40 m)	429	-0.019	0.981	-0.16 to 0.12
Depth (>40–60 m)	205	0.352	1.422	0.18 to 0.53
Depth (>60–80 m)	93	0.503	1.653	0.26 to 0.75
Depth (>80 m)	359	0.969	2.635	0.79 to 1.15
Distance to coast ( $\leq 20$ km)	1321	–	–	–
Distance to coast (>20–40 km)	111	0.659	1.932	0.44 to 0.88
Distance to coast (>40–60 km)	45	1.223	3.396	0.87 to 1.57
Distance to coast (>60 km)	87	2.192	8.951	1.88 to 2.50

During summer walrus dived to the sea bottom regularly (Fig. 8). In contrast, dives to the sea bottom were seldom in wintering/breeding areas (Fig. 8) or when in transit to/from them (Fig. 8), indicating little or no benthic feeding in such areas.

## DISCUSSION

A number of new aspects of walrus natural history were revealed by this study and some previous suggestions, based on observations of one or a very few individuals, regarding wintering behaviours were confirmed. During the summer season walrus in Svalbard used coastal, shallow waters, similar to other areas within the species' range. During this non-breeding season, walrus would be expected to seek out places with abundant food resources near areas with appropriate haulout platforms for resting. The coastal areas of Svalbard clearly provide both. The diving behaviour of the studied walrus demonstrated that most of the dives performed during summer reached the sea floor, suggesting intensive feeding activity during this period. Note that, although these walrus spend approximately 25 % of the time hauled out during summer (Lydersen et al. 2008), the long FPTs observed in this study close to the coast and in shallow waters were independent of whether the time spent hauled out was included in the analysis or not.

The fact that walrus populations exhibit strong site fidelity with regard to summering haulout sites, over extended periods of time, has been known for thousands of years; this behaviour has been actively exploited by northern people who have hunted walrus for generations (Fay 1982). However, the present study has confirmed suggestions made previously that it is not just a population level phenomenon. All of the walrus in this study that were tracked for periods in excess of a year showed fidelity to previously used feeding areas in consecutive years. Homing behaviour, i.e. the use of a previously occupied home range, has been reported previously for Pacific walrus (Jay & Hills 2005) and for 1 male Atlantic walrus in Greenland (Born et al.

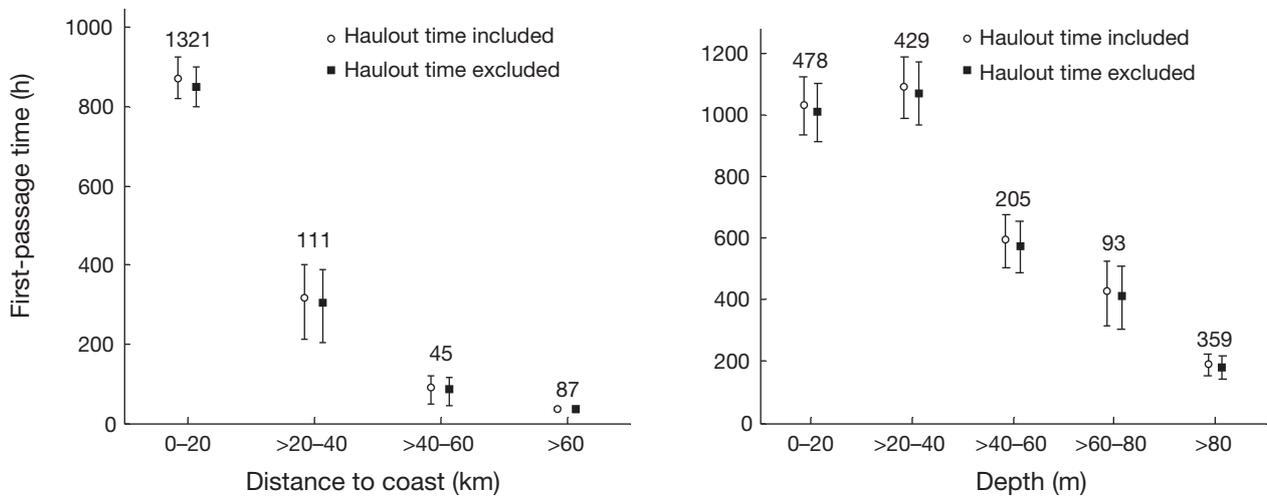


Fig. 7. *Odobenus rosmarus*. Bootstrapping means and 95% confidence intervals (CI) of the first-passage time (40 km radius) at distinct distances to the coast (left panel) and depth (right panel) for male walrus in Svalbard, during the summer/non-breeding season. Means and CIs are given, both including and excluding the time walrus spent hauled out on land or ice. Numbers of locations within each category are displayed above each CI line

2005). This behaviour is perhaps not surprising given that the food resources (bivalves and other benthic invertebrates) of walrus are relatively predictable in a spatial sense compared to pelagic food resources, which are highly dynamic in space and time (Sims et al. 2008). Knowledge gained via experience in finding food resources in particular areas is likely at least a partial cause for the observed fidelity by individual walrus. Some of the walrus in this study moved significant distances from the wintering/breeding areas back to the summering/feeding areas. The navigation mechanisms used by walrus are unknown, but walrus have been reported to follow the same migration route in different years, independent of sea ice concentrations (Born et al. 2005). The only walrus tracked in this study during 2 consecutive wintering seasons showed fidelity to the previous year's breeding area. Similar fidelity to a wintering/breeding area was also reported for 1 walrus in Greenland (Born et al. 2005).

This study identified areas that are probably used as breeding locations, based on movement and diving patterns of the male walrus. Most of these areas were located between the northeast corner of Svalbard and FJL. Although walrus from Svalbard and

FJL are known to belong to the same population (Born et al. 1995, Andersen et al. 1998), and movements of male walrus from Svalbard to FJL have been previously observed outside the breeding season (Wiig et al. 1996), this is the first time that movements to FJL during the breeding season have been conclusively

Table 5. *Odobenus rosmarus*. Estimated coefficients ( $\beta$ ), hazard ratios ( $e^\beta$ ) and 95% confidence intervals (CI( $\beta$ )) for wintering/breeding areas for walrus from Svalbard for the mixed-effects Cox proportional hazards model selected according to the AIC<sub>c</sub>. Numbers of locations in each category are also given (n). Note: A  $\beta$ -value  $>0$  ( $e^\beta >1$ ) indicates an increased risk of leaving, while a  $\beta$ -value  $<0$  ( $e^\beta <1$ ) is interpreted in the opposite way

Variable	n	$\beta$	$e^\beta$	CI( $\beta$ )
Depth ( $\leq 20$ m)	50	–	–	–
Depth ( $>20-40$ m)	33	-0.354	0.702	-1.37 to 0.66
Depth ( $>40-60$ m)	55	-0.683	0.505	-1.55 to 0.18
Depth ( $>60-80$ m)	71	-0.309	0.734	-1.15 to 0.54
Depth ( $>80$ m)	425	0.246	1.279	-0.55 to 1.04
Month (Jan)	157	–	–	–
Month (Feb)	121	-0.218	0.804	-0.51 to 0.08
Month (Mar)	68	-0.023	0.977	-0.37 to 0.33
Month (Apr)	62	-0.313	0.731	-0.71 to 0.09
Month (May)	35	0.091	1.095	-0.46 to 0.64
Month (Jun)	26	1.048	2.852	0.53 to 1.57
Month (Oct)	32	1.728	5.630	0.81 to 2.64
Month (Nov)	52	-1.056	0.348	-1.61 to -0.51
Month (Dec)	81	-0.369	0.691	-0.76 to 0.02
Ice concentration (0–20%)	24	–	–	–
Ice concentration ( $>20-40\%$ )	21	-1.226	0.293	-2.12 to -0.34
Ice concentration ( $>40-60\%$ )	24	-0.573	0.564	-1.46 to 0.31
Ice concentration ( $>60-80\%$ )	72	-0.916	0.400	-1.81 to -0.03
Ice concentration ( $>80-100\%$ )	301	-1.234	0.291	-2.13 to -0.34

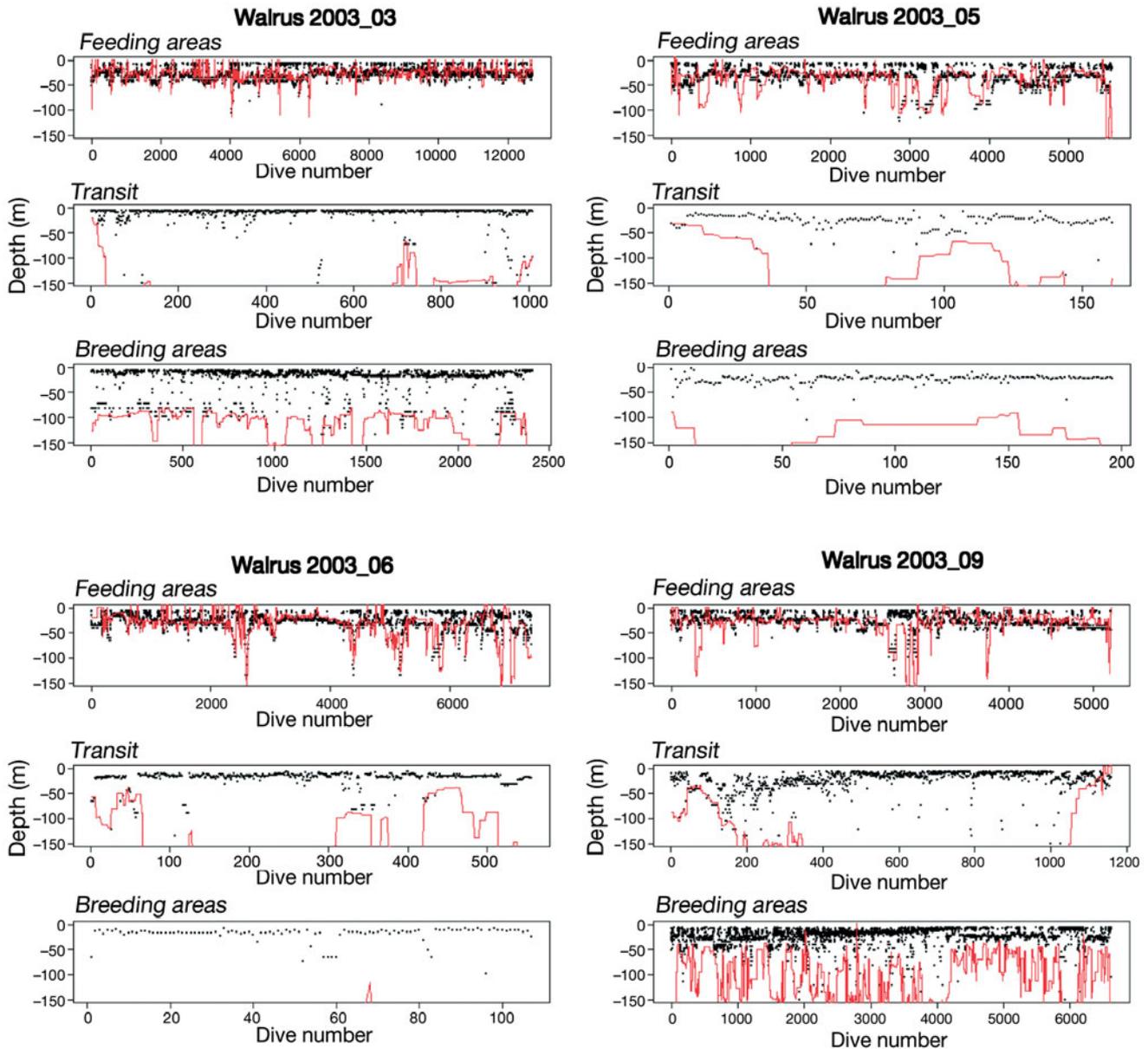


Fig. 8. *Odobenus rosmarus*. Maximum depth of the dives recorded for 4 of the tracked walruses in summering areas, wintering areas and when in transit between such areas. Sea bottom depth ( $\leq 150$  m) is also shown (red line). Dives that extend below the sea floor are due to either animal location errors, or more likely, lack of precision in the bathymetric data

documented. Interestingly, walrus feeding in the south of Svalbard during summer usually travelled to FJL or to the pack ice between the 2 archipelagos, while walrus summering in the north of Svalbard did not go all the way to FJL, even though the distance is shorter for these individuals. This is probably because females can be found closer at hand. Female walrus have been observed in the northeast corner of Svalbard during summer (Gjertz & Wiig 1994; C. Freitas, K. M. Kovacs, M. A. Fedak and C. Lydersen pers. obs.), so it is very likely that male walrus summering in the north of the archipelago are aware of their presence. A

previous study by Wiig et al. (1996) reported trips by male walrus from Svalbard to FJL outside the breeding season, and these were interpreted as reconnaissance trips for females. One individual in this study performed 1 such out-of-season trip. However, this male did not return to the areas visited in the autumn during the breeding period, at least prior to March when this individual's transmitter ceased functioning.

The male movement patterns observed in the present study support the conjecture that breeding in this population occurs mainly between January and March, and perhaps extends later into the spring; this

latter point could not be tested with rigor because several of the SRDLs ceased to transmit during the spring. Atlantic walrus in Greenland and Canada also breed mainly between January and April (Mansfield 1966, Sjare & Stirling 1996, Born 2001, 2003), although sexually active males can be found from November to July (Mansfield 1958, Born 2003) and females in oestrus can be found from January to June (Born 2001). The mating system in walrus has been described as a lek or a female-defence polygyny system (Fay et al. 1984, Sjare & Stirling 1996), where females and calves haulout on the ice or rest in the water, while males station themselves alongside female groups and perform complex, stereotyped underwater songs (Fay 1982, Fay et al. 1984, Sjare & Stirling 1996). In the Atlantic it seems that a single male has exclusive access to a small herd during a given period of time (1 to 5 d), after which it is replaced by another male, with some males attending the female herds significantly more often than others (Sjare & Stirling 1996). The invasion of a male's display area can result in agonistic displays and sometimes intensive fights (Fay 1982, Fay et al. 1984, Sjare & Stirling 1996). It is possible that males move to breeding areas before females become reproductively active, to establish themselves in areas where the different groups of females are located, to interact with potential competitors and perhaps also to establish dominance relationships so that they can attempt female attendance as early as is possible.

Walrus in the Pacific are thought to follow the seasonal advances and retreats of sea ice throughout the year (Fay 1982), and the same pattern has been assumed to be followed by Atlantic walrus, because these animals can only break through ice up to about 20 cm thick (Born et al. 1995). However, 1 individual tracked by Born et al. (2005) in Greenland during winter used waters with extensive ice coverage (>90%). Similarly, this study also provides evidence that walrus use areas with very extensive ice cover (>90%), as far as 600 km from ice-free areas. It should be noted that drifting ice, identified by remote sensing as >90% ice concentration, still provides significant amounts of open water and does not necessarily imply the need to break through thick sea ice to breathe at the surface. Other species, such as white whales *Delphinapterus leucas*, which cannot break through thick ice, have been reported to move distances of 700 km through areas of >90% ice cover (Suydam et al. 2001).

The intensities of habitat use by walrus both during transit to, and when in, breeding areas were independent of water depth and distance to the coast. Because offshore areas were frequently ice covered, access to resting platforms was not a constraint. The areas where males concentrated their time during the winter breeding season were considerably deeper than within

their summer feeding areas. Fay (1982) suggested that male Pacific walrus fed very little during the breeding season. The diving behaviour analysed in this study from the time when walrus were in the winter offshore areas reveals that male walrus do not often dive to the sea bottom at this time. This suggests that feeding activity was probably very limited while they were in breeding areas. However, female Pacific walrus do feed during the winter/breeding period according to Fay (1982), especially if they are pregnant or lactating. It is therefore somewhat surprising that the males in this study were in such deep areas during the breeding season, when they were presumably attending females. There are no data on female locations during winter for this population, but the observed male movements at the time when breeding is known to occur for walrus suggest the presence of females in those areas. It might be that the presence of closely packed drift ice in those areas provides a more stable environment for females and their calves, compared with more open ice areas, such as those found in the marginal ice zones. It might also be that diving and foraging at depths >100 m is not a constraint for female walrus. Little is currently known about the water masses seasonally in these areas, so it is not possible to determine what environmental attributes beyond the ice quality might be involved in determining wintering areas.

In summary, the over-wintering movements of the study walrus revealed that during the Arctic winter, male Atlantic walrus actively travel through areas of dense ice cover; they do not follow the sea ice advances and retreats. The main breeding areas for the Svalbard/FJL population are located in ice-covered waters between northeast Svalbard and FJL, as was hypothesised by Wiig et al. (1996). Breeding seems to occur mainly from January to March (and maybe into April). Walrus habitat use changes markedly between seasons. In summer, habitat use appears to be driven by the feeding needs in combination with available haulout areas, which includes land and also summer pack-ice whenever it is available in coastal areas, though this is not common (K. M. Kovacs & C. Lydersen pers. obs.); summer habitat use is strongly affected by water depth and distance to the coast. Winter habitat use seems to be driven by breeding needs and was, in this study, independent of water depth and distance to shore. Males seem to feed little during the breeding season and their habitat selection is probably mainly affected by the presence of females. Seasonal site fidelity seems to be strong from year to year in both summer and winter for individual walrus. This study has advanced our knowledge regarding movement patterns and habitat selection, particularly in winter, for male walrus, but many questions remain unan-

swered. Potential geographic differences in movement patterns need to be explored and a much broader geographical area needs to be studied with the new satellite technology. Tagging female walrus in the near future will be essential in order to develop a more complete understanding of the winter ecology of this species. The females' location choices presumably determine the winter distribution of males; and females face more complex habitat choices because of their need to feed throughout the year, including times when they are pregnant or nurturing young. One ongoing problem for habitat assessment work in remote regions is that environmental data are often quite limited in such areas, where even fundamental marine data such as bathymetry are missing for large geographic sectors. However, these data are likely to improve rapidly in the near future. The safe-handling procedures developed during this study programme for walrus, as well as the more broadly applicable advances in tracking technologies and spatial analyses, make it more feasible/justifiable to work with male and female walrus in the future. Some of these latter developments are also relevant for other large marine mammals in remote, changing regions, where satellite-tracking technologies are certain to permit more complete assessments of the ecology of these species in the decades to come.

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