Movements of walruses (*Odobenus rosmarus*) between Central West Greenland and Southeast Baffin Island, 2005–2008

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ABSTRACT

Between 2005 and 2008, 31 walruses were tagged with Argos satellite transmitters at their wintering grounds at Store Hellefiske Banke, Central West Greenland (N=23), and at their summering grounds off the coast of Southeast Baffin Island, Canada (N=8). Two male walruses moved along the Greenland coast from Store Hellefiske Banke north to Disko Banke, where contact was lost. Two other males went further north, up to the Upernavik area. Contact was lost with one of these tags, but the other animal travelled southward again and went towards Southeast Baffin Island. Eight of the tagged walruses moved between West Greenland and Baffin Island, demonstrating a connection between walruses at these sites. Walruses left the Store Hellefiske Banke during the period 7 April to 17 May and on average used 7 days to swim the 400 km across Davis Strait. The migration routes were quite similar; they travelled over the shallowest areas at the narrowest part of the strait. The timing of the spring dispersal and migration towards Canada was closely linked to the extent and timing of the retreat of the pack ice edge. One flipper tagged male that was marked off South Baffin Island was recovered in a hunt on Store Hellefiske Banke, documenting that the reverse migration also occurs. Off West Greenland satellite tagged walruses spent a lot of time around the Store Hellefiske Banke (55.0°–56.5° W), using this shallow area as feeding grounds irrespective of the ice cover in this area. Partial sexual segregation was observed. Despite a tendency in West Greenland for males to occur farther offshore, farther from the ice edge and at greater depths, only their preference for denser ice cover (64% ice cover) differed significantly ($P=0.019$) from the habitat preferences of females (52% ice cover). Coast dispersal was more condensed and the segregation between males and females was more pronounced during autumn along the Southeast Baffin Island. Females remained farther north ($P<0.001$) and farther east ($P=0.006$), and males were more often located offshore in areas with greater water depths ($P=0.024$). Males had also had larger home range than females during both seasons.

INTRODUCTION

Walruses occur during the winter and spring in Central West Greenland (between ca. 66.50° and 70.75° N), but are absent from this area during the open water period (i.e. summer; Born et al. 1994). Walruses in Central West Greenland are to a large extent genetically and geographically separate from walruses farther north (i.e. the Baffin Bay stock in the Smith Sound area; Andersen et al. 2014), but do not differ genetically from walruses along SE Baffin Island across Davis Strait (Andersen et al. 2014, NAMMCO 2009). When in Central West Greenland the walruses' preferred habitat are two banks (<200 m) with suitable food items: West of Disko Island (69.75° to 70.75° N) and Store Hellefiske Banke (66.50° and 68.25° N; Born et al. 1994). However, prior to this study no information on the movements of walruses from these two banks to the sites they occupy during the open water period has been available.

Understanding the movement and stock discreteness of walruses is important for several reasons. Walruses are subsistence hunted in both Central West Greenland and along Southeast Baffin Island in Canada. Historical and current exploitation rates are relatively high and are thought to be unsustainable in the long-term (Born et al. 1994, 1995, NAMMCO 1995, 2006, Witting and Born 2005, COSEWIC 2006). Understanding stock structure and stock identity is important for calculating population sizes and for setting levels of sustainable exploitation appropriate to specific stocks (e.g. NAMMCO 2005, 2009, Heide-Jørgensen et al. 2014, Stewart et al. 2014). Information about movements obtained from satellite telemetry is an important tool in developing an understanding of stock delineations.

The walruses in West Greenland are likely to soon face negative impact from increased industrial activity. Oil exploration has been intensified in recent years in walrus habitat in West Greenland (Mosbech et al. 2007). Noise from seismic surveys, exploration drilling, building of production facilities and other traffic related disturbances linked to oil exploration activities including helicopter transport and intensified shipping may potentially displace walruses from their wintering grounds on Store Hellefiske Banke, Disko Banke or other important feeding grounds. Oil spills pose another risk because they can affect the benthic feeding of the walruses, which may force the walruses to seek food in suboptimal regions. A change in ice extent is also likely to affect the movement and behaviour of the walruses. Sea ice in eastern Baffin Bay has decreased significantly during the last decade (Stirling and Parkinson 2006). Continuation of this trend in eastern Baffin Bay may not only influence the distribution of walruses but also the human hunting patterns, providing the hunters easier access to walruses on their near-shore foraging grounds (Born 2005). In future, warmer winters may change the distribution and migration pattern of ice-associated species like the walrus.

Satellite telemetry can provide insight into the seasonal range of the walrus, their migration routes, their feeding areas as well as their relationship to the physical environment, including water depth and ice conditions. During 2005–2008, we deployed satellite tags on a total of 23 walruses at their wintering grounds in Central West Greenland and on 8 walruses at their summering grounds on the coast of Southeast Baffin Island in 2007. The study was designed to collect information on: 1) local movement and habitat choice by walruses in West Greenland to produce impact assessments related to oil exploration (Boertmann et al. 2009); 2) large-sale movement and stock discreteness to determine sustainable harvest levels in West Greenland and Nunavut in Canada (NAMMCO 2009); 3) walrus haul-out and diving activity to determine correction factors to be applied in aerial survey assessments in the West Greenland stock (Heide-Jørgensen et al. 2014) and; 4) the seasonal range of the walrus, their migration routes, their feeding areas as well as their relationship to the physical environment including water depth and ice conditions. In this paper we present details on objective 2 and 4 based on information from 31 tagged walruses in the West Greenland and Southeast Baffin Island area during 2005–2008.

MATERIAL AND METHODS

The tagging areas

During March–April 2005–2008, satellite transmitters were attached to walruses on Store Hellefiske Banke, which extends from ca. 66.00° to 68.25° N and from 53.25° to 56.83° W; this area has water depths ranging from 20 to 200 m. This bank is frequented by walruses during spring when they feed primarily on bottom dwelling molluscs (Born et al. 1994). Additionally, in late August–early September 2007 satellite transmitters were deployed on walruses that were hauled out on land on Southeast Baffin Island between Cumberland Sound and Cape Dyer (c.a. 64.83° to 66.75° N and from 61.00° to 63.66° W). Along this coast there is also a shelf with shallow waters (<200 m).

Tagging of the walruses

During the tagging at Store Hellefiske Banke a 19.4 m (64 feet) 72 GRT (Gross register tonnage) steel fishing vessel, *Nanna L.* (GR 08-062), with home port in Sisimiut, West Greenland, was used for searching for walruses in the pack ice 40–80 nautical miles from the coast. In many cases walruses were approached and tagged from this vessel. However, if the ice situation permitted a 5.2 m (17 foot) fibreglass dinghy with a 6 or 30 Hp engine was used to approach the walruses. During the tagging on Southeast Baffin Island, the *Nanna L.* was used as a base camp for tagging operations conducted on land. An 8.5m (28 foot) aluminium boat with two 125 HP motors was used to conduct the daily trips to and from the haul-out sites.

Instrumenting the walruses

Thirty one walruses were tagged in West Greenland in 2005 (N=3), 2006 (N=5), 2007 (N=6) and 2008 (N=9) and in Canada during 2007 (N=8; Table 1). Four transmitter types were used. Three types were implanted into the skin of unrestrained walruses (implant tag, the puck tag and the matchbox tag), while the animals were either hauled out on pack ice or were swimming. The fourth, which was used on Southeast Baffin Island, was mounted on the tusk of tranquilized animals (tusk tag).

Implant tag

Three walruses (2005) were equipped with implant tags (2.0 × 1.0 × 9.6 cm) similar to those described in Jay et al. (2006; Fig. 1a). A modified airgun was used for the deployment following the methods outlined in Heide-Jørgensen et al. (2001).

Puck tags

Ten walruses (2006: 5; 2007: 5) were equipped with puck tags (5.2 × 2.8 cm puck-shaped disc) similar to those used by Jay et al. (2006; Fig. 1b). In Greenland they were mounted on the tip of an arrow (carbon shaft balanced with an internal lead rod) and were delivered by use of a compound crossbow (185lb PSE Wiper Mojave, Crossbows4u, UK). In Canada, they were delivered using a traditional hunting harpoon on which the harpoon tip on the transmitter replaced the usual harpoon tip.

Match box tag

These transmitters were rectangular epoxy cast transmitters (2.9 × 1.8 × 4.0 cm) of the SPOT-5 type (Wildlife Computers, Redmond, Washington, USA) mounted with a harpoon head/anchor (Fig. 1c). They were deployed using a CO_2-powered rifle (Model IM, DanInject, www.daninject.com) equipped with a telescopic sight. The transmitters were attached to the skin of the walruses using a 6.5 cm long harpoon head-like stainless steel anchor.

Tusk tag

These tags (10 cm long × 6 cm in diameter) were developed by SMRU (University of St Andrews,

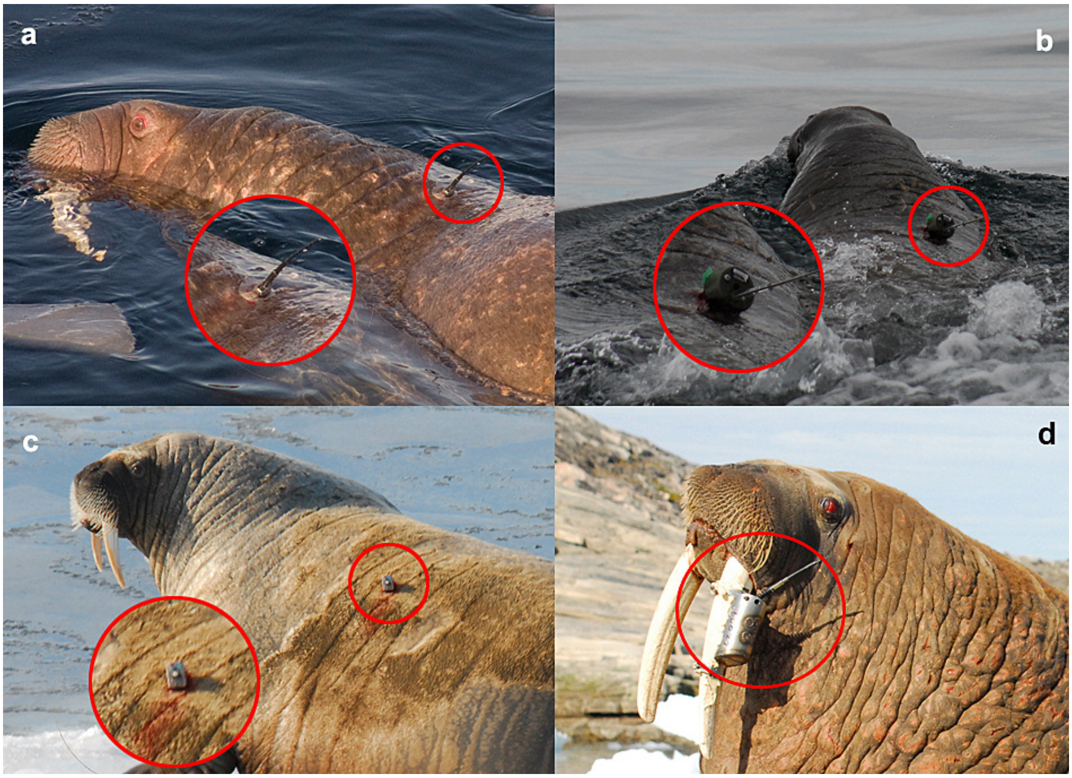

Fig. 1. Four types of transmitters used during the walrus tagging between 2005 and 2008 In Greenland and Canadian waters. a) Implant tag from Wildlife computers, b) Puck tag from Telonics, c) Matchbox tag from Wildlife Computers and d) Tusk tag from the Sea Mammal Research Unit, University of St Andrews. Transmitters highlighted within red circles.

Scotland) and deployed as described by Lydersen et al. (2008; Fig. 1d, see further details in Lydersen et al. 2008). The walruses were immobilized during the tagging operations on Southeast Baffin Island using Ketamine and Medetomedine (Zolapine; Maddox et al.2007). The drugs were delivered intramuscularly by a DAN-INJECT CO_2 Injection Rifle, equipped with a telescopic sight. All immobilized walruses were also fitted with orange Jumbo Roto Tags in each hind flipper.

The harpoon anchors of the three implant tag types were developed by Mikkels Vaerksted, Vallekilde, Denmark (www.mikkelvillum.com). The primary "target" site was the medial back/thorax region in order to obtain signals while animals were at sea, when the walruses surface to breathe (Fig. 1c). During tagging the sex and the length of the tusks (estimated or measured from gum line to tip along the frontal curvature) were noted. The tusk length was used for age classification (Table 1).

Data collection and analysis

Data on movements and transmitter status were collected via the Argos Location Service Plus system (Toulouse, France; Harris et al. 1990). All location fixes were used in the present study after being filtered by a SAS-routine, Argos_Filter V7.02 (Douglas 2006). The filter settings for this study were - maximum swim speed - 10 km/h (minrate=10) and all other settings were set as by the defaults. The speed setting resulted in locations leading to swim speed > 10 km/h being excluded. If however the distance between locations was less than 5 km (maxredun=5), they

Table 1. Information on 31 walruses instrumented with satellite-linked transmitters at Store Hellefiske Banke during March–April 2005–2008 and at Southeast Baffin Island August–September 2007. Bold text indicates animals that were tracked across the Davis Strait. Bold and italics indicates animals that were re-sighted after the transmitter had stopped. Brackets indicate intermediate destinations.

Tagging Year and # tagged animals	Tag ID	Sex	Tusk Length (cm)	Estimated Age (years)	Tag Type	Tagging latitude	Tagging longitude	Tagging date (D/M/Y)	Date of last transmission	Tag duration (days)	Tracking distance (km)	Number of obtained positions	End (intermediate) destination
2005 WG										*107*	*1506*	*90*	
	2005-56572	Male	30	14	Implant	68.250N	56.040W	25/3/2005	1/4/2005	7	86	4	SHB
	2005-56573	**Female**	**30**	**14**	**Implant**	**68.250N**	**55.250W**	**25/3/2005**	**30/5/2005**	**66**	**1145**	**60**	**SEB**
	2005-56574	Male	50	24	Implant	68.209N	56.106W	26/3/2005	29/4/2005	34	275	26	SHB
2006 WG										78	2533	253	
	2006-17763	Male	25	11-12	Puck	67.743N	55.984W	19/3/2006	26/3/2006	7	235	36	SHB
	2006-17765	Male	8	2-3	Puck	67.743N	55.984W	19/3/2006	12/4/2006	24	410	47	SHB
	2006-56571	Male	12	4-5	Puck	67.976N	56.244W	21/3/2006	11/4/2006	21	871	82	SHB
	2006-56570	Female	28	13	Puck	67.683N	54.999W	22/3/2006	6/4/2006	15	223	41	SHB
	2006-56574	Male			Puck	67.992N	55.696W	26/3/2006	6/4/2006	11	794	47	DB
2007 WG										186	2887	258	
	2007-56570	Male	15?	5-7	Matchbox	67.693N	54.880W	10/4/2007	17/4/2007	7	121	5	SHB
	2007-56573	**Female**	**25?**	**10-12**	**Matchbox**	**67.648N**	**55.147W**	**11/4/2007**	**17/8/2007**	**128**	**1999**	**106**	**SEB**
	2007-56574	Male	15?	5-6	Matchbox	67.683N	54.987W	10/4/2007	23/4/2007	13	136	9	DB
	2007-17567	***Female***	***15?***	***5-6***	***Puck***	***67.635N***	***54.842W***	***10/4/2007***	***30/4/2007***	***20***	***183***	***39***	***SHB/SEB***
	2007-17759	Male	38?	18-20	Puck	67.813N	54.852W	10/4/2007	24/4/2007	14	271	75	SHB
	2007-57100	Male	10?	4-5	Puck	67.658N	54.842W	10/4/2007	14/4/2007	4	177	24	SHB
2007 SEBI										324	7451	824	
	2007-08198	Male	10	20+	Puck	67.970N	63.417W	10/4/2007	9/9/2007	18	449	10	SEB
	2007-02508	Female	20	9	Puck	65.600N	62.573W	22/8/2007	28/8/2007	5	41	3	SEB
	2007-60021	Male	30	14	Tusk	65.648N	62.478W	23/8/2007	12/10/2007	48	889	96	SEB
	2007-60022	Male	37	17	Tusk	65.648N	62.478W	25/8/2007	30/10/2007	66	1960	147	SEB
	2007-60023	Female	25	11	Tusk	65.948N	62.257W	25/8/2007	3/11/2007	65	1397	161	SEB
	2007-60024	Female	29	13	Tusk	65.648N	62.257W	30/8/2007	7/11/2007	69	1136	189	SEB
	2007-60026	Male	41	19	Tusk	65.066N	63.239W	30/8/2007	18/9/2007	15	314	23	SEB
	2007-60027	***Male***	***40+***	***19+***	***Tusk***	***65.066N***	***63.239W***	***3/9/2007***	***11/10/2007***	***38***	***1264***	***195***	***SEB/SHB***
2008 WG										***334***	***7766***	***341***	
	2008-56570	**Female**	**30**	**13-14**	**Matchbox**	**67.773N**	**54.640W**	**3/9/2007**	**29/5/2008**	**57**	**793**	**32**	**SEB**
	2008-56571	Male	35	10+	Matchbox	67.698N	54.650W	2/4/2008	26/4/2008	24	259	13	SHB
	2008-56572	Calf	6	3	Matchbox	67.693N	54.812W	2/4/2008	3/6/2008	62	1555	83	UPV
	2008-56573	**Female**	**L:20 R:15**	**10**	**Matchbox**	**67.687N**	**54.988W**	**4/4/2008**	**29/4/2008**	**25**	**1045**	**17**	**SEB**
	2008-56574	Male	12-15	6-7	Matchbox	67.675N	54.886W	2/4/2008	1/5/2008	29	448	10	SHB
	2008-57098	Male		5-6	Matchbox	67.590N	54.782W	2/4/2008	3/5/2008	31	641	28	SHB
	2008-57099	Female	L:6 R:20	10	Matchbox	67.631N	54.710W	4/4/2008	5/4/2008	1	26	9	SHB
	2008-57100	**Male**		**5**	**Matchbox**	**67.675N**	**54.003W**	**4/4/2008**	**7/6/2008**	**64**	**1858**	**112**	**(UPV) SEB**
	2008-57101	**Male**		**20+**	**Matchbox**	**67.772N**	**55.045W**	**4/4/2008**	**15/5/2008**	**41**	**1141**	**37**	**(SEB) SHB**
All										***1029***	***22142***	***1766***	

SHB: Store Hellefiske Banke; DB: Disko Bay; UPV: Upernavik; SEB: South East Baffin Island

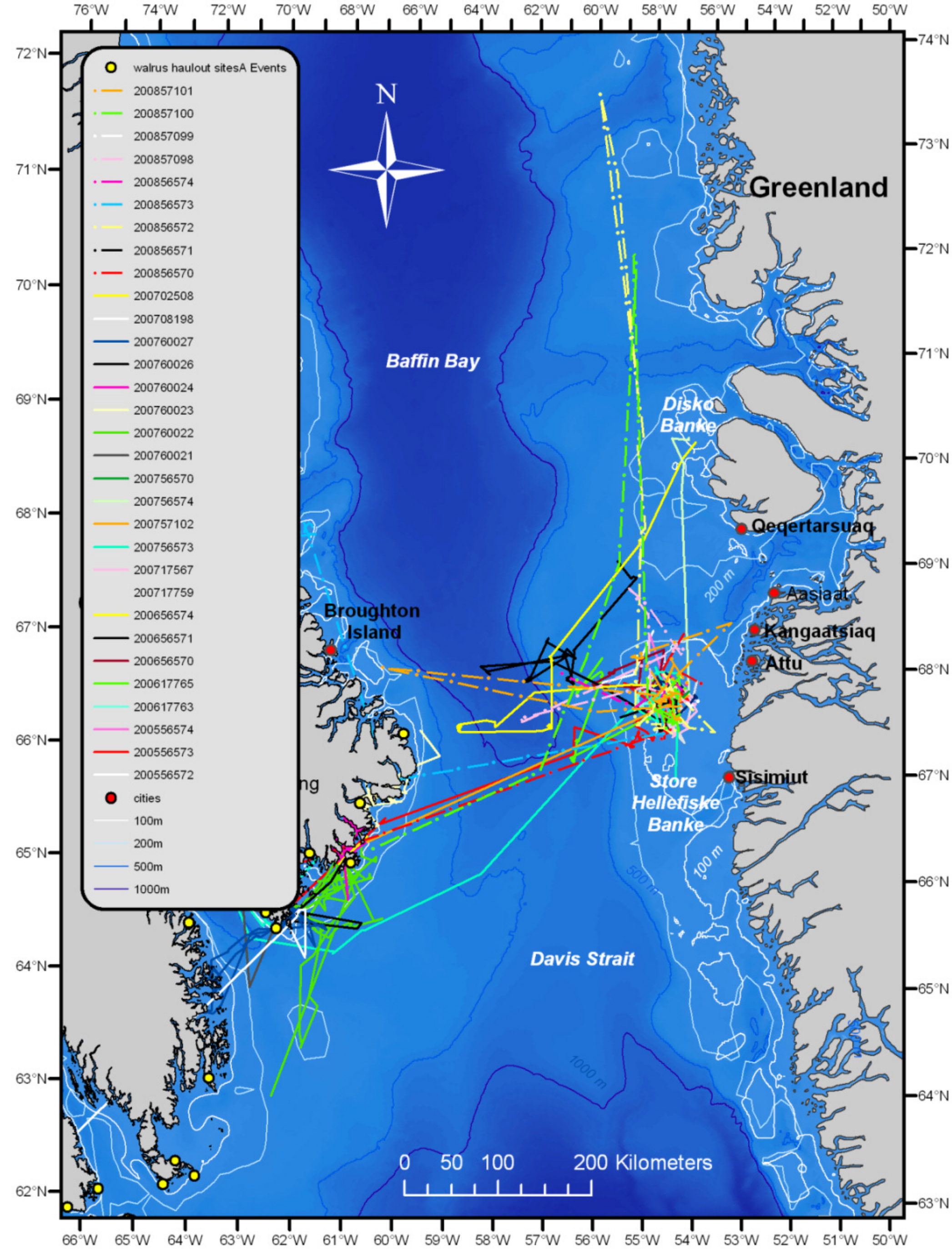

Fig. 2. Tracklines from 31 walruses tagged with satellite-linked transmitters at Store Hellefiske Banke in West Greenland (WG) during March–April 2005–2008 and at Southeast Baffin Island (SEB) August-September 2007. Of these, 6 transmitters lasted long enough to show the spring migration across northern Davis Strait to the Canadian summering grounds of Southeast Baffin Island. One transmitter which was deployed in WG was re-sighted on SEB after it had stopped transmitting. Additionally, three walruses crossed the mid-sector line between Canada and Greenland during their spring movements but returned to WG where transmissions stopped.

were both retained, because the swim speed calculations may be unrealistic due to the respective inaccuracies of the close positions (for details see Sveegaard et al. 2011).

The Argos Filter V7.02 was used to calculate the distances travelled and the migration speed.

Sea Ice Concentration Data
We used the Sea Ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data from the National Snow and Ice Data Center (NSIDC) in Boulder, CO (Cavalieri et al. 1996). This product is designed to provide a consistent time series of sea ice concentrations (the fraction, or percentage, of ocean area covered by sea ice) spanning the coverage of several passive microwave instruments. The data are provided on a polar stereographic grid with a nominal cell size of 25 x 25 km. Temporal coverage is daily during the SSM/I era (1987–present) and every other day during the SMMR era (1978–1987). The uncertainty in the sea ice concentration in each cell is about 5–10% during the cold seasons (fall, winter, spring) but larger in summer when the surface contains melt water (Comiso and Parkinson 2008).

Statistical analyses
We wanted to examine the potential effects of sex, season and year on distribution. We therefore applied a linear mixed effects model using maximum likelihood estimation with distribution parameters (longitude, latitude, speed, depth, distance from land and from ice and ice coverage) as dependent variables, individual as a random or grouping factor and the fixed factors sex, month and year. Depth data was log-transformed prior to analyses to reduce skewness and a square root and arc-sin transformation were used to convert ice percentage coverage to an approximately normal distribution as recommended in Zar (1996). The model was successively reduced for non-significant factors at a 5% significance level evaluated by the likelihood ratio test. The statistical analyses we performed with the software R (R Development Core Team, 2008). Differences in tag longevity between transmitter types were analysed by an ANOVA followed by a Tukey Kramer Post Hoc test. Differences in tag longevity between sex and tusk length between tagging areas were examined using t-tests. One matchbox tag (#2008-57099) reported data for only one day and was hence not included in the longevity calculations.

SAS V9.1.3 for windows was used to run the Argos Filter. Excel 97 (SR2), SAS Enterprise Guide V4.2 and StatView V5.0.1 were used for statistical analysis and graph presentations. Maps were generated using ArcMap V9.3. The bathymetrical depth contours are based on 1-degree resolution GEBCO data V1.00. Hawth's Analysis Tools V3.27 was used as an extension to ArcMap to generate track-lines, Kernel Home Range and area calculations. To avoid autocorrelation, only one location was sub-sampled from each of the days selected for the duty cycle, for the Kernel Home Range Analysis and for the linear mixed effect models described above. Statistical analyses of habitat choice were performed with the software R (R Development Core Team 2008).

RESULTS

Duration of contact and tag type comparison
The transmission life of tags varied greatly among types, ranging from 7 to 128 days (Table 1). Puck tags had the shortest average duration (average: 14 d; range: 4–24 d), significantly shorter than the Tusk tags (average: 50 d; range: 15–69 d) and Matchbox tags (average: 44 d; range: 7–128 d), but they were not significantly different from the Implant tags (average: 36 d; range: 7–66 d; Table 1 and 2). Despite longer average duration of the Tusk tags these were not significantly different from the Matchbox or the Implant tags (Table 2). The longest lasting single tag was a Matchbox tag that transmitted for 128 days. There were too few data to rigorously examine longevity of the individual tag types by sex and season. However, the remotely deployed tags

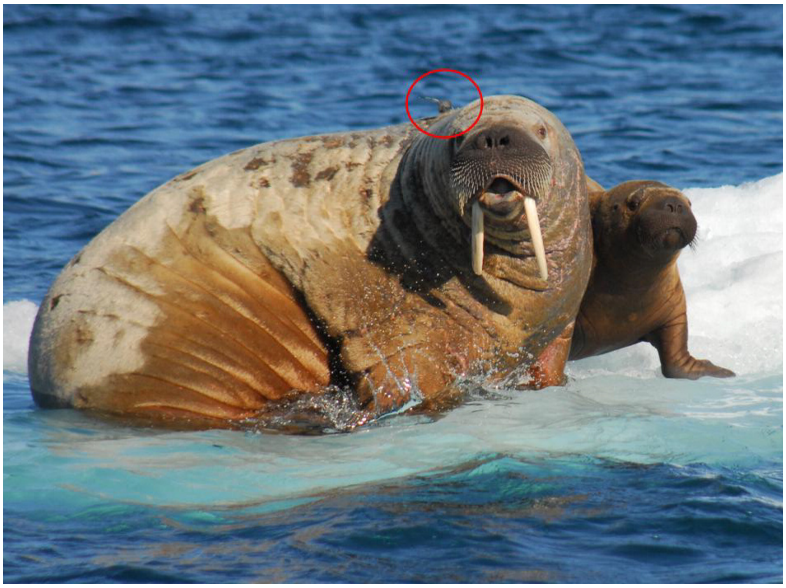

Fig. 3. *An adult female walrus re-sighted 23 August 2007 in the narrow strait north of Kekertuk Island (65.62° N/ 62.00° W), Southeast Baffin Island with a calf of the year and a Puck tag still attached on its back (within red circle) after 135 days. The tag was deployed on 10 April 2007 (#2007-17567), and stopped transmitting on 30 April 2007.*

Fig. 4*. Walrus male #2007-60027 tagged off South East Baffin Island on 3 Sept. 2007 at 65.07° N, 63.24° W, Upper photo, with flipper tag (#41), which was recovered from a walrus shot in the pack-ice of West Greenland on 24 of April 2009 (67.20° N, 55.20° W; lower photo).*

(Implant, Matchbox and Puck tags) mounted during spring lasted significantly (P=0.0282; t-test) longer on female walruses (average: 52 d; N=6) than on males (average 22 d; N=15).

Movements

Of the 23 transmitters deployed at Store Hellefiske Banke in spring (2005–2008), five lasted long enough to document migration across the northern part of Davis Strait to the Canadian summering grounds of Southeast Baffin Island (Fig. 2; Table 1). A sixth animal (#2008-57101) left West Greenland, but turned back on 9 May before reaching Southeast Baffin Island (at 67.49° N; 62.57° W), after which the transmitter stopped six days later on 15 May back on Store Hellefiske Banke (at 67.57° N; 55.13° W). An adult female walrus (#2007-17567) tagged on 10 April 2007 with a puck tag, which stopped transmitting on 30 April, was re-sighted on 23 August 2007 near Kekertuk Island (65.62° N; 62.00° W) off Cumberland Peninsula (Fig. 3.) Another three walruses crossed the midline between Canada and Greenland during their spring movements. None of the 8 tags deployed on walruses on Southeast Baffin Island in August–September 2007 lasted long enough to document potential emigration from the tagging area. However, a flipper tag (#41) deployed on a male walrus (#2007-60027) on Southeast Baffin Island on 3 Sept 2007 at 65.07° N; 63.24° W was recorded on a shot animal in the pack-ice off West Greenland at 67.21° N; 55.20° W on 24 April 2009 (Fig. 4). This observation documents migration of walruses from Southeast Baffin Island to Central West Greenland and supports the results of a shared population from the genetic studies of Andersen et al. (2014).

Within Greenland two male walruses (# 2006-56574 and 2007-56574) moved from Store Hellefiske Banke northward up to Disko Banke, but as the tags only lasted 11 and 13 days respectively, it was not possible to determine whether they stayed in this area, moved farther north, or returned. Two other male walruses (# 2008-57100 and 2008-56572) passed Disko Island and went as far north as the Upernavik area. Both subsequently turned southward on 23 May and one (#2008-57100) continued from its farthest north point (67.21° N; 55.20° W) towards Southeast Baffin Island (64.80° N; 64.11° W) where contact was lost 7 June 2008. The other walrus (#2008-56572 — a 3 year old calf accompanying its mother when tagged) returned from its farthest north position (73.26° N; 59.67° W) southward to a position northwest of Disko Island (70.25° N; 57.05° W) where contact was lost on 3 June 2008.

Most of the positions from walruses tracked to or along the Canadian coast were observed east

Table 2. Comparison of the longevity of the four tag types deployed on 30 walruses (#2008-57099 left out) instrumented with satellite-linked transmitters at Store Hellefiske Banke during March–April 2005–2008 and at Southeast Baffin Island August–September 2007. Types that were not significantly different are denoted by the same letter.

	Tag duration (days)					
Tag Type	Average	StdDev	Min	Max	N	Tukey-Kramer and Fisher PL SD post Hoc comparisons
Puck Tag	13.9	7.0	4	24	10	B
Implant Tag	35.7	29.5	7	66	3	A,B
Match box	43.7	33.8	7	128	11	A
Tusk	50.2	21	15	69	6	A
Grand Total	**34.3**	**27.9**	**7**	**128**	**30**	

** One transmitter (2008-57099) lasting only 1 day was left out (average with all Matchbox units: 40.2 days)*

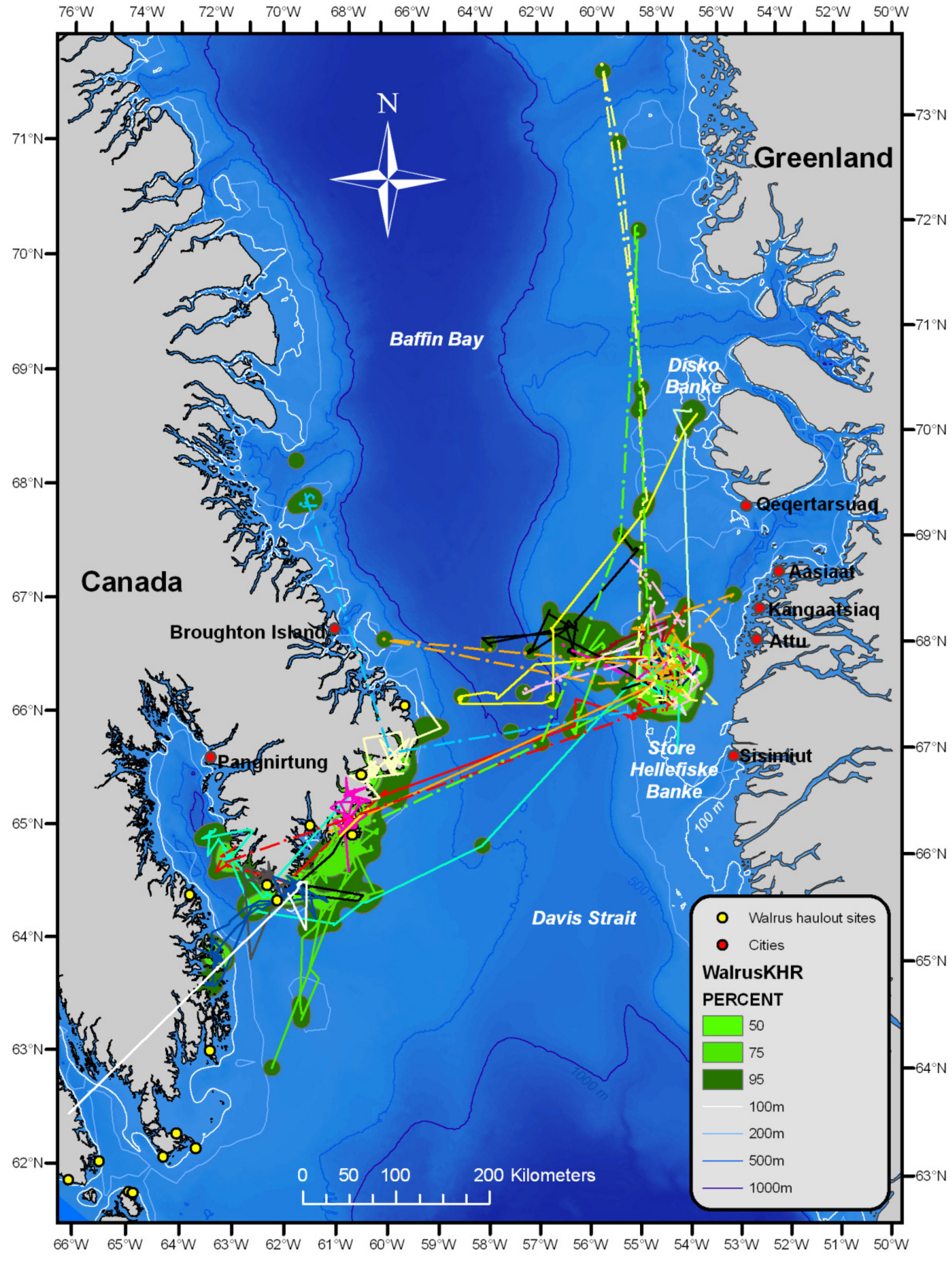

Fig. 5. Tracklines and Kernel Home Range polygons from 31 walruses instrumented with satellite-linked transmitters at Store Hellefiske Banke during March–April 2005–2008 and at Southeast Baffin Island in August–September 2007.

of Cumberland, Southeast Baffin Island. Two adult female walruses (# 2005-56573 and 2007-56573) entered 60 to 80 km into Cumberland Sound along the northern coast in 2005 and 2007. In 2005 the fjord was entered on the 10th of May by the female walrus, that had just crossed the Davis Strait, and she remained in the fjord until 30 May, when contact was lost. The other female visiting the fjord in 2007 likewise crossed the Davis Strait and entered the fjord on 18 May where it stayed until 9 July, migrating north along Southeast Baffin Island. An adult male that ranged farther from shore (up to 40 km) also spent time along the northern coast in 2007 using the fjord from 7 September to 12 October when contact was lost. An adult male (# 2007-60027) tagged in 2007 along Southeast Baffin Island crossed the Cumberland Sound southward twice and explored the northeastern coast of Hall Peninsula from 8–13 September and from 28 September to 11 October when contact was lost. The southernmost positions were obtained from an old male (# 2007-08198) with worn tusks that moved all the way down to Frobisher Bay (62.47° N; 66.66° W) where contact was lost 9 September 2007. Areas of declining preference are indicated by the calculated 50, 75 and 95% kernel home ranges depicted in Fig. 5.

Timing of the westward migration

The initiation of the movement away from Store Hellefiske Banke toward Southeast Baffin Island took place between 7 April and 25 May 2008 (N=4) indicating some variation in the timing of the departure (at least 48 days difference) within the same year. This time span also encompassed the single departures recorded in 2005 and 2007. In general the duration of traversing Davis Strait lasted between 6 and 9 days with arrivals at East Baffin Island taking place between 15 April and 31 May (Table 3). The average daily travelling distances ranged between 36 and 55 km.

Comparisons of male and female distributions

When at Store Hellefiske Banke in March–April the average swimming speed of male walruses (N=14) did not differ significantly from that of females (N=7), several of which were accompanied by calves (Table 4). Furthermore, although the calculated average positions indicated that males occurred farther offshore to the northwest over deeper water and deeper into the ice their distribution did not differ significantly from that of females (Table 4, Fig. 6). However, males did generally occupy significantly denser ice habitats (64% vs 52% ice cover, P=0.019, Table 4).

During the open water period (September–October) along East Baffin Island male and female walrus had similar swimming speeds (P=0.589; Table 4). However, all four distribution parameters differed significantly between the two sexes. Male walruses were distributed farther west and farther south than the females. In addition they were distributed in deeper water and ranged farther from land than the females (Table 4, Fig. 6).

Table 3. Calculated migration times and trip parameters for six instrumented walruses, which left West Greenland and crossed Davis Strait and arrival in Southeast Baffin Island (SEB). Italics indicates a walrus that returned to West Greenland after having reached the Canadian coast.

Tagging year	Tag ID	Sex	Estimated age (years)	Date of departure WG (D/M/Y)	Date of arrival SEB	Traversal duration (days)	Migrated distance (km)	Average daily distance (km)
2005	2005-56573	Female	14	29/4/2005	6/5/2005	7	309	44
2007	2007-56573	Female	10-12	9/4/2007	18/4/2007	9	496	55
2008	2008-56570	Female	13-14	27/4/2008	3/5/2008	6	308	51
	2008-56573	Female	10	7/4/2008	15/4/2008	8	292	37
	2008-57100	Male	5	25/5/2008	31/5/2008	6	326	54
	2008-57101	*Male*	*20+*	*1/5/2008*	*9/5/2008*	*8*	*299*	*37*
Average						7	338	46

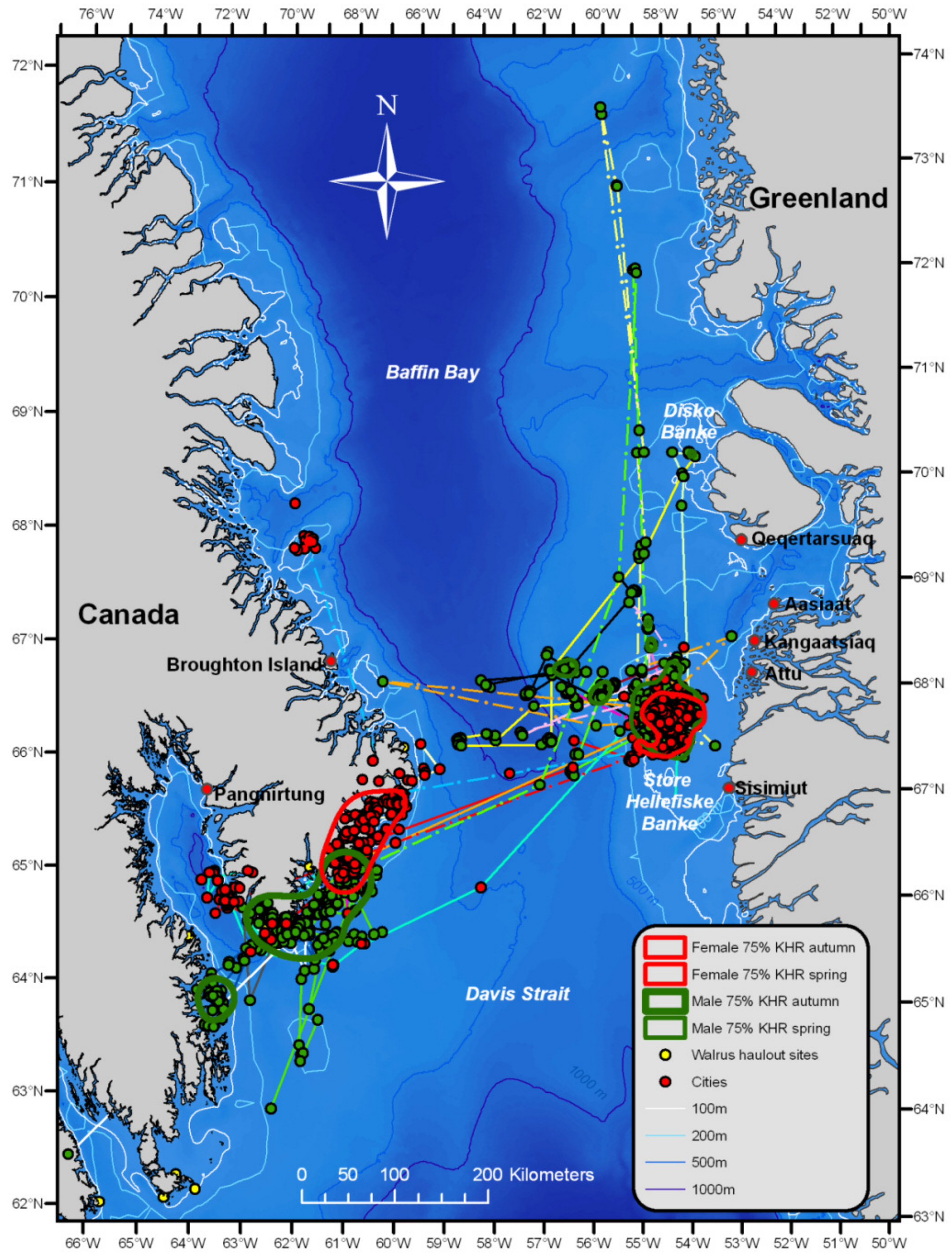

Fig. 6. Positions for the entire period and Kernel Home Range Polygons (75%) during spring and autumn for 20 male and 11 female walruses instrumented with satellite-linked transmitters at Store Hellefiske Banke during March–April 2005–2008 and at Southeast Baffin Island August–September 2007.

The 75% Kernel polygon for males during the spring period was 9542 km^2, which was ca. 70% larger than that of females (5623 km^2, Fig. 6). Similarly the 75% Kernel polygon for males during the autumn period was ca. 84% larger for males (5931 km^2) than for females (3218 km^2). Both sexes were more dispersed in spring than in the autumn. Males used 1.6 times and females 1.7 times larger areas in spring than autumn.

Monthly differences in behaviour and distribution

During spring walruses in the Store Hellefiske Banke area were distributed significantly ($P<0.001$) farther west, farther south, at greater depths, farther away from land, farther away from the ice edge but in lighter ice conditions in March compared to April (Table 4). However, there was no difference in swimming speed between these two months. During the autumn walruses along Southeast Baffin Island also showed differences in distribution as the walruses in October were farther east, farther south and over slightly greater depths compared to the September distribution (Table 4, Fig. 7). There was no difference in swimming speeds or distance from land.

Interannual differences in distribution in Central West Greenland

Significant differences ($P<0.001$) between years (2005–2008) were found for walrus distribution in Central West Greenland relative to longitude, bathymetry, distance to land and ice cover. The walruses stayed farthest west in 2006 (57.35° W; 67.61° N) and had the largest average distance to land (121.9 km) and were present over the greatest average depths (442.1 m depth; Table 4; Fig. 8). In contrast, the walruses stayed furthest east in 2007 (55.42° W; 67.64° N) with the shortest average distance to land (66.0 km) and over the shallowest depths (72.6 m; Table 4; Fig. 8). In 2007, the walruses were in the highest average ice density (72.8%) and in 2005 in the lowest (32.1%; Table 4; Fig. 8). No inter-annual differences were detected for swimming speed or distribution relative to latitude or the ice edge.

Walrus distribution relative to changing ice conditions

In order to understand the seasonal patterns of the west to east movement of the walruses, ice data were extracted for all days of the four years the walruses were tracked at 67.5° N (Fig. 8). In all four years the walruses were present east of the dense pack ice (average=23.5% concentration; range of means: 0–81.6%) with the majority of observations distributed between 55.0° and 56.5° W. Most of the later westward movement occurred in dense ice (>50% concentration) on the western side of Davis Strait south of 67.5° N.

We calculated the daily mean sea ice concentration on Store Hellefiske Banke at depths less than 200 m for the years 1979 through 2010. Figure 9 shows the annual cycle of sea ice on the bank. To investigate the timing of ice retreat in the spring, we selected a threshold of 20% concentration and calculated the date each spring, when the sea ice concentration fell below the threshold. We found a trend of −7.6 days per decade (significant at 99%, $p<0.01$), indicating that sea ice break-up is occurring one week earlier per decade on average, but with large inter-annual variability (standard deviation 12.6 days per year). Since the walrus tracking data only spans the period from 2005 to 2008, the number of years (and animals) is too limited to establish a relationship between the timing of westward migration and ice conditions, but the trend toward earlier spring sea ice retreat may be a factor on decadal or longer time scales.

DISCUSSION

Duration of contact and tag type comparison

The average duration of the puck (14 d) and the implant (36 d) tags deployed in the pack ice in West Greenland was comparable to the average longevities for walruses that were tracked in the Bering Sea (20 and 22 days, respectively; Jay et al. 2006). The matchbox tags clearly have a sub-

Table 4. Regional and sex related comparisons and means of distribution parameters of walrus tagged in West Greenland that travelled to Southeast Baffin Island (2005–2008). "P-values (**P<0.05**) are given for likelihood ratio tests of reducing linear mixed effect models including the factor listed and with individual walrus as the grouping variable.

Differences in	Sex			Month			Year				
Central West Greenland	**P**	**Females**	**Males**	**P**	**March**	**April**	**P**	**2005**	**2006**	**2007**	**2008**
Speed (km/h)[1]	0.675	7.6	9.3	0.379	9.1	8.9	0.892	6.7	8.6	9.7	9.3
Longitude	0.457	-55.5	-56.22	**<0.001**	-56.71	-55.94	**<0.001**	-55.67	-57.35	-55.42	-55.44
Latitude	0.249	67.54	67.63	**<0.001**	67.55	67.63	0.438	67.56	67.61	67.64	67.61
Bathymetry (m)	0.359	-80.9	-229.1	**<0.001**	-299.0	-176.2	**<0.001**	-93.5	-442.1	-72.6	-86.5
Distance from land (km)	0.677	71.9	90.0	**<0.001**	87.8	85.8	**<0.001**	79.8	121.9	66.0	68.8
Distance from ice edge (km)	0.690	21.0	23.9	**<0.001**	26.8	22.6	-0.299	7.8	25.6	26.3	23.4
Presence in ice cover (%)	**0.019**	51.6	64.0	**<0.001**	48.7	63.8	**<0.001**	32.1	62.8	72.8	59.7
Southeast Baffin Island	**P**	**Females**	**Males**	**P**	**September**	**October**	**2007[3]**				
Speed (km/h)[1]	0.589	4.1	4.0	0.171	4.3	3.5					
Longitude	**0.006**	-62.33	-63.38	**<0.001**	-62.95	-62.88					
Latitude	**<0.001**	64.98	66.01	**<0.001**	66.40	65.48					
Bathymetry (m)	**0.024**	-18.6	-93.2	**<0.001**	-59.9	-60.8					
Distance from land (km)	**<0.001**	1.5	8.8	**0.111**	4.2	8.6					

Comments:

[1]Speed calculated for consecutive positions in the time window between 0.5 and 5 hours

[2]Depths below 2000 m are not included

[3]Year not included in the modes as the animals were only monitored in 2007

[4]Land observations excluded

stantial potential for longer transmissions compared to the other remotely deployed tags as one tag lasted as long as 128 days. Premature transmission stops in the matchbox transmitters is likely due to tearing out of the skin or damage to the units (antenna breakage or electronic failures) as the walruses move through the dense pack ice and haul out on ice during the spring. This conjecture is supported by our observation that males inhabiting denser pack ice in spring had shorter tag lives than females. The short-lived tags (down to 1 and 7 days) may have succumbed to either extreme behavior of single individuals, less successful deployments in terms of tag placement and anchor operation, or transmitter failure. Tusk tags deployed in this study in Southeast Baffin Island had significantly shorter longevity (50 days) than similar tags deployed at Svalbard (278 days; Freitas et al. 2009). It is uncertain to what extent the differences were caused by the haul-out and bottom substrate (rock versus sand), the age of the tags after production when deployed (2.5 year vs 0.5 year), the attachment, the size of the tusks or other reasons. The walrus male (#2007-60027; flipper tag #41) that was tagged on Southeast Baffin Island in September 2007 and shot in the pack-ice of West Greenland in April 2009 had lost its tusk tag and broken the right tusk on which the tag had been mounted (Knud Lennert pers. comm.). Smaller tusks may be more likely to break. Tusks in our study averaged 34 cm (range: 25–41 cm) in length, significantly smaller (t-test, P=0.003) than the Svalbard animals' tusks (mean: 43 cm, range: 34-53 cm; Freitas et al. 2009).

Tags of all types may last longer on female walruses than males because they occupy less dense ice and generally have a less "vigorous" behavior (Table 4). The main part of the study was conducted during the walrus mating season, which peaks between January and April (e.g. Fay 1982,

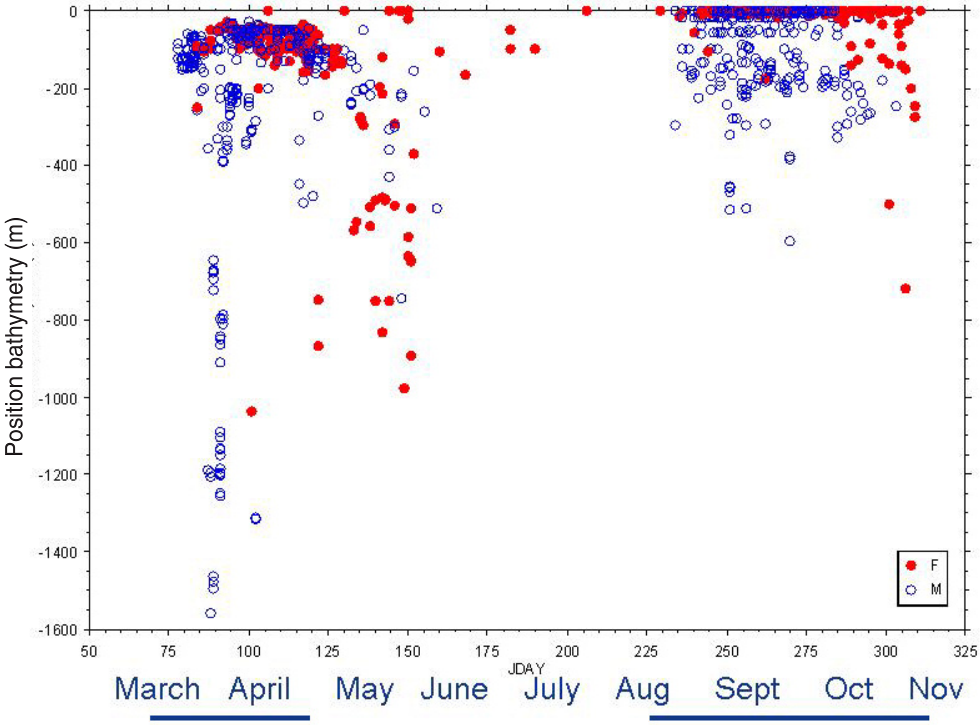

Fig. 7. *Water depths at the positions reported for 20 male (blue) and 11 female walruses (red) relative to Julian Day and season. The walruses were instrumented with satellite-linked transmitters at Store Hellefiske Banke during March–April 2005–2008 and at Southeast Baffin Island in August–September 2007. Bars indicate spring and autumn definitions used in the text.*

Sjare and Stirling 1996, Born 2001, 2003) when adult male walruses engage in ritualized displays in the water and sometimes engage in physical fights with competing males (Sjare and Stirling 1996, Born pers. observation). During the tagging operations, we documented that the general pattern was that male walruses occupied denser ice farther west of Store Hellefiske Banke at greater depths, compared to females which were often accompanied by calves. Male walruses were more active, travelling farther west, farther from land, and exploring larger regions.

Movements

In Central West Greenland, walruses winter at two near-shore foraging grounds: the southern ground in the Sisimiut–Aasiat area and the northern one off the west coast of Disko Island/Qeqertarsuaq. These two shallow areas, with suitable benthic food, are separated by the entrance to Disko Bay where water depths exceed 200 m and where walruses are generally absent (Born et al. 1994; Heide-Jørgensen et al. 2014). The present study documented a connection between these two foraging grounds and that walruses from the Southeast Baffin Island–West Greenland complex winter at both Store Hellefiske Banke and Disko Banke.

It has been suggested that walruses that occur in West Greenland south of Melville Bay (i.e. south of ca. 75° N) belong to the “West Greenland stock”. However, based on distribution, timing of migration and catches, walruses wintering along the western coast of Disko Island and farther north may represent the southern extreme of the North Water sub-population, whereas those occurring farther south belong to the West Greenland stock (cf. Born et al. 1995). Genetic studies indicate that walruses from Disko Island and farther north have only limited—and mainly

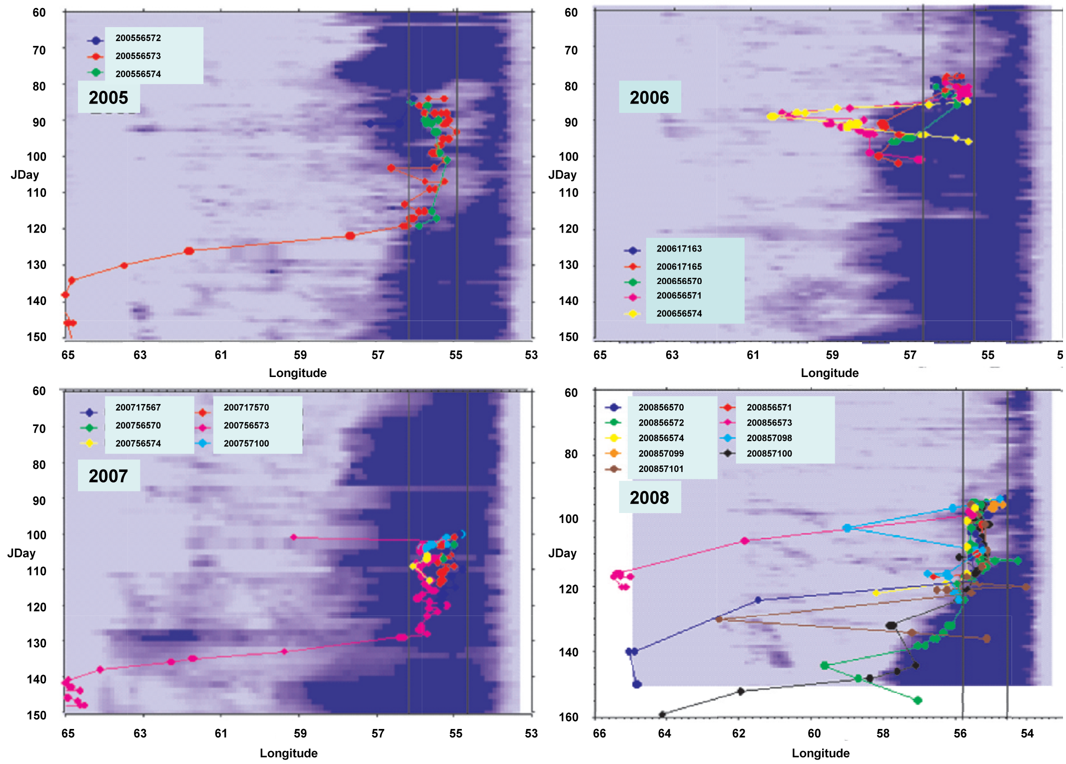

Fig. 8. *Longitudinal movements of individual walruses across the Davis Strait from 68.0° to 64.5° N relative to Julian Day (JDay) for spring deployments in 2005–2008 with longitudinal 100% ice coverage (white) and open water (blue) shown for 67.5° N.*

male mediated—contact with the population of walruses at Store Hellefiske Banke and that in Northwest Greenland, i.e. the northern Baffin Bay population (Andersen and Born 2000, Born et al. 2001, Andersen et al. 2014). Samples for analyses are not available from the area between Disko Island and Melville Bay and hence the genetic identity of walruses in this area has not been determined.

In the present study two males moved north offshore from Store Hellefiske Banke to the Upernavik area to between 72.00° and 73.45° N, although they both returned south and one migrated to Southeast Baffin Island. Hence, the present study indicates that during spring at least some walruses from the Baffin Island–West Greenland complex temporarily occur north of Disko. Annual variation in the amount of sea ice in eastern Baffin Bay may influence walrus movements along the West Greenland coast. Hence, due to low sample size no firm conclusion can be reached from the present study concerning the demographic affinity of the walruses occurring along the coast between Disko Island and ca. 76° N (Heide-Jørgensen et al. 2014).

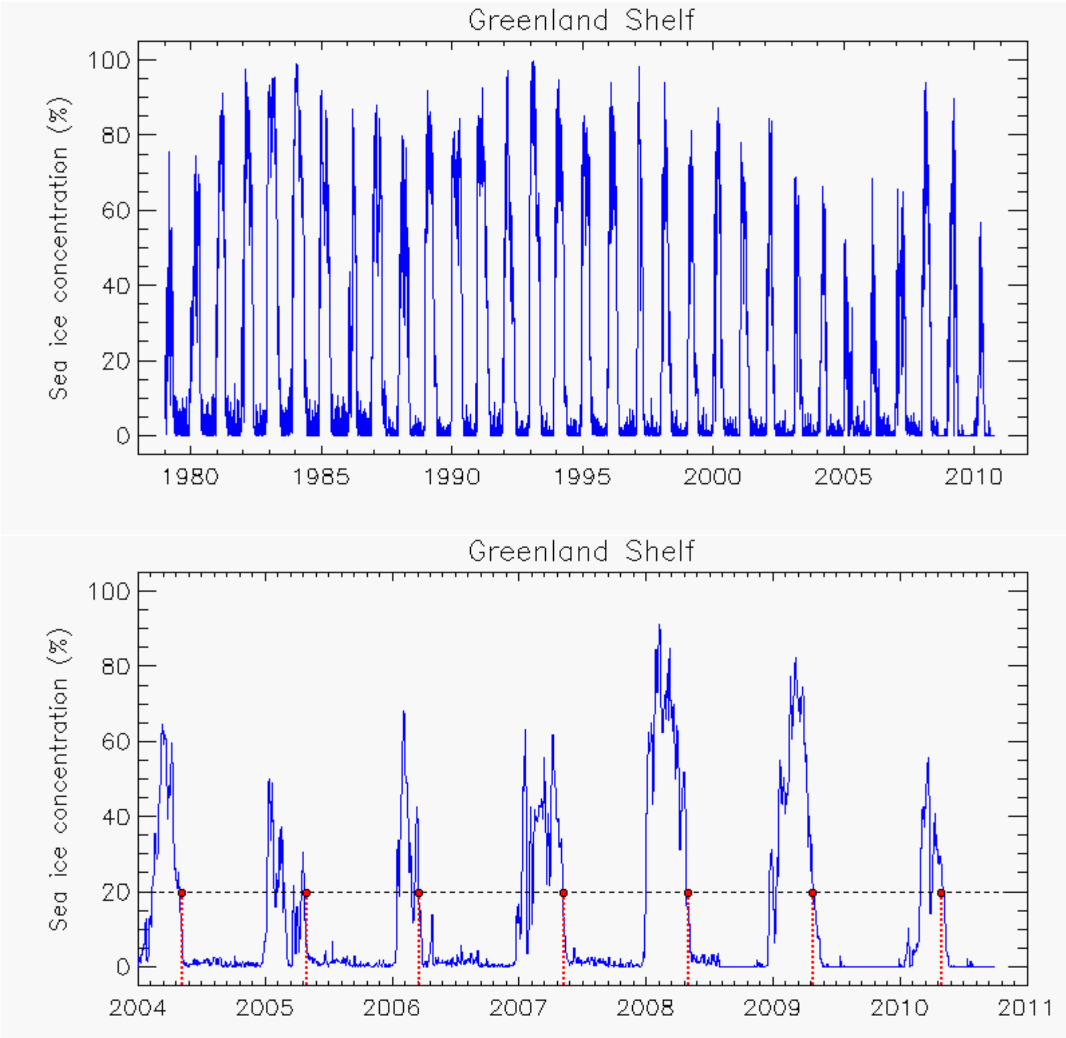

***Fig. 9**. Sea ice concentration on Store Hellefiske Banke from 1979 to 2010 (top) and from 2004 to 2010 (bottom). The red vertical dotted lines indicate when the sea ice concentration falls below 20% (black horizontal dashed line).*

A link between walruses in Central West Greenland and Baffin Island has been suggested previously (cf. Born et al. 1995 for a review). Scattered observations summarized by Born et al. (1994, 1995) of walruses in the middle of Davis Strait from May to July suggested that walruses cross Davis Strait from Greenland to southeastern Baffin Island. This connection between West Greenland and Southeast Baffin Island was supported by genetic studies which suggest that the two areas contain animals from a single population (Andersen and Born 2000, Andersen et al. 2009, Andersen et al. 2014). The present study demonstrated that the link is maintained by movements in both directions by both adult males and females with calves.

Seasonal movement patterns have been shown for other walrus populations as well. Frietas et al. (2009) documented quite set annual movement patterns for 17 male walruses around Svalbard. During summer, walruses were most often found in coastal areas with a median distance to the coast of 4.6 km. During winter, most walruses performed long distance movements, reaching areas up to 840 km from the tagging locations. Walruses performed offshore winter movements between early October and early February and returned between late February and late June.

Comparison of male and female distributions

The partial segregation of the sexes is in accordance with walrus distribution in other regions (e.g. Born et al. 1995, 1997). In Southeastern Baffin Island the segregation was most expressed. Females were located farther to the north and had smaller home ranges. Adult females with calves seemed to occur more frequently at sheltered inshore haul-out sites whereas the off-shore exposed rocks facing deeper waters have a higher proportion of adult males (Pangnirtung HTA pers. comm., Stewart et al. 2014). The general occurrence in West Greenland of males farther offshore and in more dense ice than females and young has also been noted previously (Born et al. 1994). Walruses exhibit a high degree of sexual dimorphism in body size; males (weight: 1114 kg; std. length: 314 cm) are much larger than females (weight: 720 kg; std. length: 269 cm; e.g. Knutsen and Born 1994). Hence, the slightly different and only partly overlapping local distribution of the sexes at the relatively localized summering and wintering feeding (mating) grounds may represent an innate social mechanism to reduce competition for their sessile food. Furthermore, the tendency of males to occur in areas with relatively deeper waters than females and young may also reflect a greater diving capacity of the larger males. Male walruses off Svalbard often dive to depth between 100 to 150 m (Freitas et al. 2009). Jay et al. (2010) reported differences in distribution patterns for the Pacific walrus of the northern Bering Sea. In this region most adult females and young walruses use sea ice for hauling out throughout the year. In spring, they followed the receding ice pack northward to summer in the Chukchi Sea. Unlike females, most adult male walruses spend the summer months along the coast of the Bering Sea, using land haul-outs to rest between foraging trips. In autumn, the females and young walruses in the Chukchi Sea migrate with the developing sea ice southward into the Bering Sea, where in late autumn and winter they are joined by the males that summered in this area (Jay et al. 2010).

Walrus distribution relative to ice conditions and feeding areas

The factors determining the timing of walrus migrations from West Greenland are unclear. Although not documented in this study, walruses spend the winter both in West Greenland and along Southeast Baffin Island (see Born et al. 1995, Stewart 2008, Andersen et al. 2014). Basic requirements for walruses in wintering grounds are, apart from access to air, access to food and mating partners (Sjare and Stirling 1996). The West Greenland banks are known to host walrus food items such as the bivalves *Mya truncata, Serripes groenlandicus, Hiatella arctica* and *Macoma baltica* (cf. Born et al. 1994, Born 2005). The present study and Born et al. (1994) both indicate that the preferred percentage ice for walruses in West Greenland is 50-60% with some variation according to sex, season and year. In the Svalbard–Franz Josef Land region some walruses winter in very dense pack ice (Freitas et al. 2009). Walruses are unable to break through ice that is thicker than about 20 cm (Fay 1982) but in both West Greenland and Southeast Baffin Island shallow polynya and pack-ice areas with dynamic leads exist where walruses can overwinter.

Our study showed that during spring periods from 2005–2008 walruses showed greater fidelity to the geographic area on Store Hellefiske Banke than to the retreating eastern edge of the Davis Strait pack ice. This indicates that the motivation for walruses to stay at the banks is access to food rather than haul-out possibilities at the ice edge. Similarly, Jay et al. (2010) concluded that local areas of activity were independent of ice drift in the Bering Sea in spring.

The timing of the westward migration may be linked to the timing of West Greenland hunting activity. The concentration of hunters on the coast at the walrus wintering areas is high and in these areas hunting of walruses has always been of importance (Born et al. 1994, Born 2005, Witting and Born 2005, Witting et al. 2014). The catch of walrus is still relatively large (NAMMCO 2005, 2009). We suggest that the mechanism triggering the migration of walruses from West Greenland in spring is a combination of hunting activity (that to a large extent is governed by the density of ice, where less ice means easier access to the game by boat) and the seasonal decrease in sea ice itself, which gradually opens the migration route towards Southeast Baffin Island. The number of years and the small sample size of animals providing data on the onset of the westward migration is however too limited to provide conclusive data regarding a linkage between migration onset and ice conditions. In addition the individual variation of the onset of the westward migration within a single year may be substantial as the 2008 data from only four animals varied by as much as 48 days. On decadal and longer time scales, a trend toward earlier spring sea ice retreat is expected that is likely to influence the timing of migration of this walrus population.

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