# A note on a walrus' European odyssey

EW Born[1], E Stefansson[2†], B Mikkelsen[2], KL Laidre[1,3], LW Andersen[4], FF Rigét[5], M Villum Jensen[6], D Bloch[2]

[1] *Greenland Institute of Natural Resources, DK-3900 Nuuk, Greenland*
[2] *Museum of Natural History, FO-100 Tórshavn, Faroe Islands*
[3] *Polar Science Center, APL/University of Washington, Seattle, WA 98105-6698, USA*
[4] *Department of Bioscience (Aarhus University), DK-8410 Rønde, Denmark*
[5] *Danish Centre for Environment and Energy, Arctic Research Centre, Department of Bioscience (Aarhus University), DK-4000 Roskilde, Denmark*
[6] *Mikkel Villum, DK-4571 Grevinge, Denmark*

† *This paper is dedicated to the memory of Eyðfinnur Stefansson who passed away on 17 November 2011.*

## ABSTRACT

This study reports on the first successful identification of the site of origin of an extralimital walrus in Europe. On 24 February 2010 an adult male Atlantic walrus (*Odobenus rosmarus rosmarus*) migrant was instrumented with a SPOT-5 satellite-linked transmitter (SLT) while hauled out on a beach on the Faroe Islands at 62° 15′ N/06° 32′ W. This SLT transmitted until 5 March during which period the walrus made local movements, likely for feeding. Transmissions were not received during 6-25 March, however, visual observations during this time indicated that the walrus remained at the Faroe Islands. A second transmitter was deployed on the same animal on 25 March 2010 at another site on the islands (62° 16′ N/07° 04′ W). Activity data collected over 13 days indicated that the walrus hauled out in three different places in the Faroe Islands and used a total of 24% of its time resting on land. On 29 March 2010 the walrus left the Faroe Islands and headed west-northwest towards Northeast Iceland. On 2 April it took a north-northeast course and swam towards Svalbard where the last location was received from a sea ice covered area on 25 April 2010 at 78° 27′ N/09° 20′ E (i.e. ca. 40 km west of the island of Prins Karls Forland in the western Svalbard archipelago). During 29 March–22 April the walrus swam a minimum distance of 2216 km between the last location at the Faroe Islands and the first location at Svalbard, with an average swimming speed of 4.5 km/h. A genetic analysis indicated that this walrus belonged to the Svalbard–Franz Josef Land subpopulation, thereby confirming that it returned to its site of origin.

## INTRODUCTION

*"Bringing it all back home"* — Bob Dylan, 1965

Three separate subpopulations of Atlantic walrus (*Odobenus rosmarus rosmarus*) are found in the NE Atlantic Arctic: (1) The East Greenland, (2) the Svalbard-Franz Josef Land and (3) the Kara Sea–Southern Barents Sea–Novaya Zemlya subpopulation (Born et al. 1995, Andersen et al. 1998, Born et al. 2001, NAMMCO 2005).

The stenophagous and essentially molluscivorous walruses feed mainly at <100 m depth (Fay 1982, Born et al. 2003). For the majority of the year they are confined to near-shore shallow water feeding grounds along the Arctic coasts where they show a high degree of site fidelity (Born et al. 1995 and references therein, Born et al. 1997, 2005, Freitas et al. 2009).

However, extralimital records of this exclusively Arctic species have been reported from several sub-Arctic and boreal areas (e.g. Mercer 1967, Nores and Pérez 1988, Kingsley 1998). Born (1988, 1992), Gjertz et al. (1993) and van Bree (1997) summarized observations of walruses along western-northwestern European coasts during 1800–1996. Since then several observations have been made of walrus visitors along northwestern European continental coasts (Born unpublished data). Walrus visitors have also occasionally been observed in the North Atlantic Ocean at Iceland (Kristjánsson 1986, Petersen 1993, Iceland Seal Centre: www.selasetur.is) and at the Faroe Islands (Bloch 1998, Bloch et al. 2001, Anon. 2011a). Bloch et al. (2001; and Archive of Faroese Museum of Natural History) documented 14 records of walrus at the Faroe Islands (from 1895 to 2011). However, according to Anon. (2011a) a total of 17 observations representing perhaps 14 different individual walruses were made on the islands between ca. 1810 and 1998. The last sighting documented by photo in the Faroe Islands was of an adult male walrus that hauled out at the island of Nólsoy between 23 March and 1 April 1998 (Anon. 2011a, photo in Gaard et al. 2006a p. 63). The last visit prior to the one reported in this paper was in March 2001, when a young walrus (external tusk length of about 5 cm indicates that it was ca. 2 years old; cf. Fay 1982) was observed on two occasions in the Faroe Islands (Faroese Museum of Natural History unpublished data).

The geographic origin of walruses that visit Europe has long puzzled researchers and there has been a range of suggestions about stock affiliation of these vagrant individuals (e.g. Ritchie 1921, Jensen 1927, Born 1988, Gjertz et al. 1993). Until now there have been no studies tracking the movement of European walrus visitors using satellite telemetry.

In this paper we report the movements of an adult male walrus tagged with a satellite transmitter in late winter 2010 at the Faroe Islands, an area outside the general geographic range of the species. A genetic comparison was conducted between this individual and samples from walruses in subpopulations in East Greenland and Svalbard–Franz Josef Land and was used in concert with the telemetry data to confirm the area of origin of this individual.

## MATERIAL AND METHODS

### Study area

The Faroe Islands (ca. 61° 30′ – 62° 30′ N, ca. 06°– 08° W) are located on the "Greenland–Scotland Submarine Ridge" that separates the water masses in the Nordic Seas from the Northeast Atlantic Ocean (Gaard et al. 2006a). A shelf surrounds the islands with <100 m deep waters extending 20–30 km from the coast. On the shelf there are several areas with mollusc banks, in particular the northwestern, eastern and southwestern regions (Gaard et al. 2006b). At depths <100 m, suitable walrus prey are available, such as the bivalves *Mya* sp., *Cardium* sp., *Hiatella* sp. and *Serripes* sp. (e.g. Born et al. 2003, Fay 1982), several other invertebrates (e.g. snails — *Nudibranchiata*, Fay et al. 1982), and sand-eels (*Ammodytes* sp.; Born et al. 1994) are found living in 6–10 °C warm water (Bloch 2005; Gaard et al. 2006b). The islands have mainly rocky shores but also have several sheltered gravel and sand beaches.

### Instrumentation and biopsying

On 22 February 2010 an adult walrus was observed in Árnafjørður (the island of Borðoy) in eastern Faroe Islands (Fig. 1). Judging from body size, the presence of many skin tubercles, and the 40–50 cm long, stout tusks the animal was determined to be a 25+ year old adult male in good condition (Fig. 2). The media named the walrus "Ári". According to local residents of the town of Árnafjørður the animal used the gravel beach in the town for hauling out several times between foraging trips. At 02:35 a.m. local time (=GMT) on 24 February 2010 a satellite-linked transmitter, SLT (#2010-83312), was deployed on the walrus while it was hauled out at 62° 15′

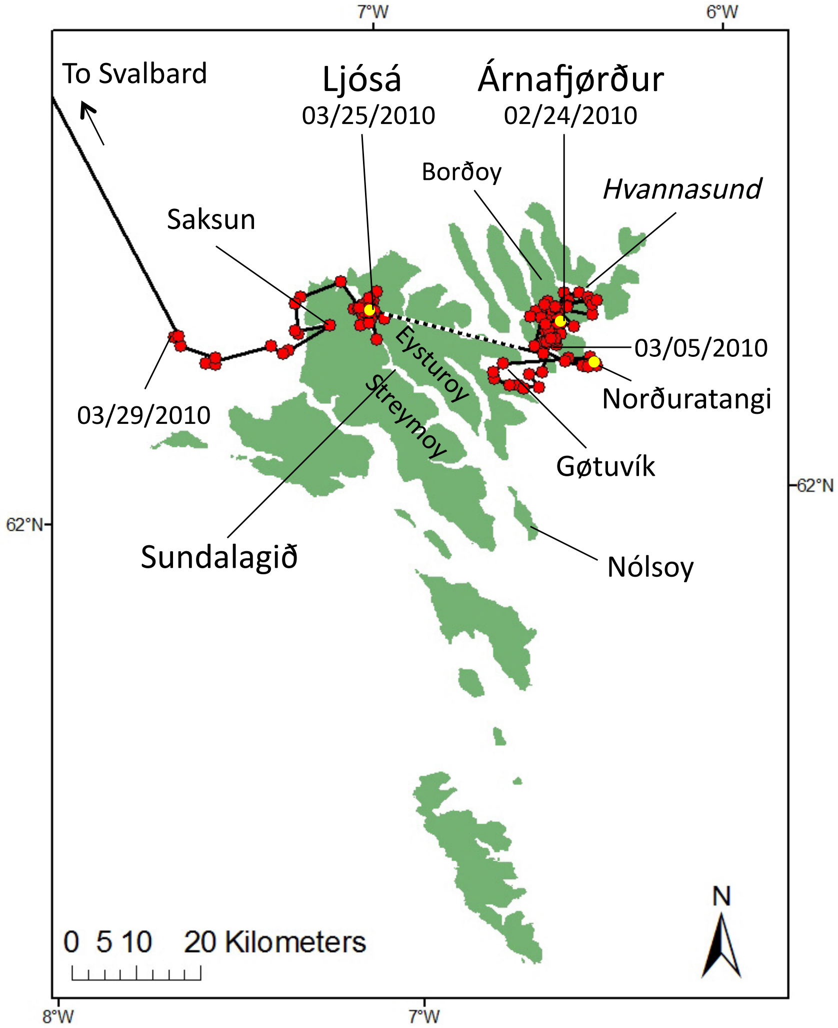



***Fig. 1.*** *Map of the Faroe Islands showing the movement of an adult male walrus that was tracked using satellite-telemetry (24 February – 5 March and 25-29 March 2010). Red dots = individual relocations from the satellite tag. Yellow dots = locations where the walrus hauled out on land during the tracking period.*

17.62′′ N/06° 32′ 05.88′′ W in Árnafjørður. In association with the deployment of the satellite transmitter, a small skin biopsy was taken using a dart fired from a $CO_2$-powered "Larsen" gun. On 25 March 2010 a second satellite transmitter (#2010-83311) was deployed at 19:15 local time when the walrus was resting on the on beach at Ljósá at 62° 16′ 02.73′′ N/07° 03′ 48.72′′ W in Sundalagið, (Fig. 1, i.e. the strait between the islands of Streymoy and Eysturoy). On this occasion the first SLT, which had stopped transmitting on 5 March, was removed. Both SLTs used were SPOT-5 "match box" transmitters (Wildlife Computers, Redmond, Washington, USA), which weighed ca. 60 g. The transmitter was fired onto the walrus using a $CO_2$-powered rifle (Dan-Inject JM Special; http://daninjectdartguns.com; Denmark). It was attached to the skin (several cm thick) using a 6.5 cm long harpoon head-like stainless steel anchor developed by Mikkel Villum (www.mikkelvillum.com; Denmark). The first transmitter was attached to the lower neck region 15–20 cm in front of the shoulders and about 20–30 cm to the right of the medial line on the back. The second transmitter was deployed ca. 10 cm behind the back of the head about 10 cm to the right of the medial line (Fig. 3).

**Data collection**

The transmitters had a transmission rate of 45 sec in water and 90 sec when the walrus was hauled out. They were both programmed to transmit continuously between 11 and 22 GMT when the salt-water switch (SWS) was dry with a maximum allowance of 150 transmissions per day. The

***Fig. 2.*** *A photo of a 25+ year-old adult male walrus that visited the Faroe Islands between 22 February and 29 March 2010. Photo: E. Stefansson*

SLTs were duty cycled to transmit every day in February–April thereafter switching to transmission every 4$^{th}$ day. Data on movement (locations) and transmitter status were collected via the Argos Location Service Plus system (Toulouse, France: www.argos-system.org).

Information on "haul-out" and "at surface time" was obtained from activity measurements from the SLT's SWS. The internal system of the SLTs continuously checked the status of the SWS ("dry" vs. "wet") every 0.25 sec and recorded the activity of the SWS in 60 min intervals. This information was stored in "timelines" (TIM) that recorded what percentage of each 60 min interval the SLT was dry. Percentage of "dry"-time/h was given in a total of thirteen increments ranging from "0%" (every measurement was wet) to "100%" (every measurement was dry). Two

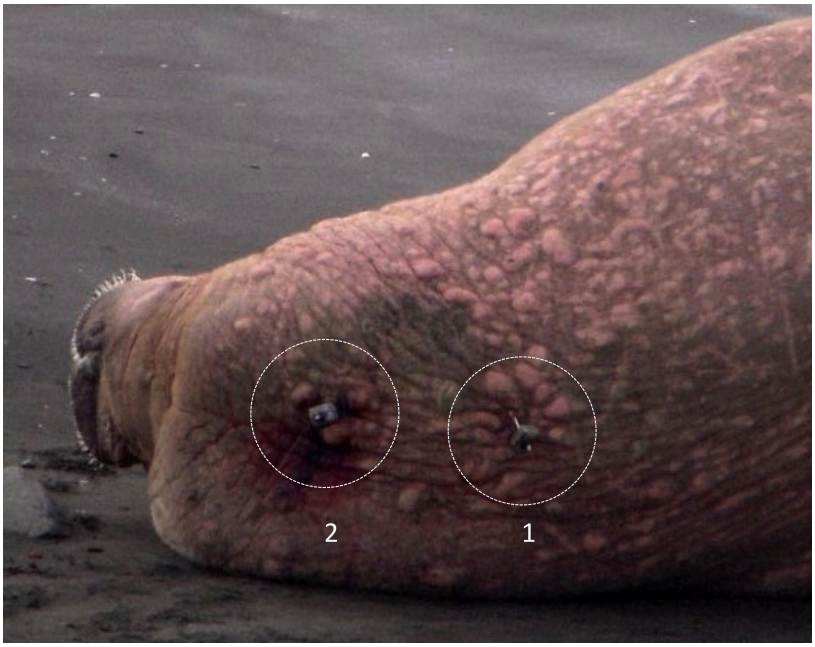



***Fig. 3.*** *The walrus while hauling out at Ljósá (Eysturoy) on 25 March 2010 with two SPOT5 transmitters. The first transmitter (1) that was deployed on 24 February stopped transmitting on 5 March 2010 and was pulled out shortly after the second transmitter (2) had been attached on 25 March 2010. Photo: E. Stefansson*

increments ranged across intervals of 5% (i.e. 0–5%; 95–100%) and nine increments ranged between 5% and 95% each covering intervals of 10%. TIMs with information on haul-out activity over a 24 h period were transmitted along with the "time-at-temperature" histograms (Wildlife Computers 2006). Temperature information was summed in four 6 h blocks (histograms) per 24 h (beginning at 0, 6, 12 and 18 h GMT). Each temperature histogram consisted of 12 user defined temperature intervals ranging from -40 °C to 60 °C. To obtain highest resolution for the range of ambient temperatures that the walrus was likely to experience when hauling out during the survey period, ten "2°C" intervals ranged between -9.9 °C and 10.0 °C.

Weather data (wind km/h, temperature °C, barometric pressure hPa, and rain (i.e. in the present case: "whether raining or not") were extracted from Landsverk ("The Faroese National Bureau of Engineering and Construction": http://www.lv.fo/database).

**Analysis of data**

*Movement*

All location quality classes (cf. www.argos-system.org) used in the study were selected with the Douglas filtering process in SAS (Argos Filter V7.02; Douglas 2006). Filtering methods and criteria are described in Dietz et al. (2014). ArcGis V9.2 and MapInfo 8.5 were used to present the maps using GEBCO bathymetry.

Total length of the track taken by the walrus between the Faroe Islands (departure from Saksun Bay at ca. 11:27 on 29 March 2010) and the final destination (arrival at ca. 11:20 on 22 April 2010) was calculated as the sum of the linear distances between all locations after filtering. Average swimming speed was calculated using two approaches: (I) As the sum of linear distances between all filtered locations divided by total time elapsed between departure from the Faroe Islands to 8 April (at 68° 37′ N/03° 55′ W) (i.e. before a long hiatus in locations until locations were received again at Svalbard; Fig. 4), and (II) total daily distance moved between daily locations (one good quality location per day) divided by time (h and min) passed between these two positions during the period 29 March–8 April 2011.

*Haul-out and at-surface activity*

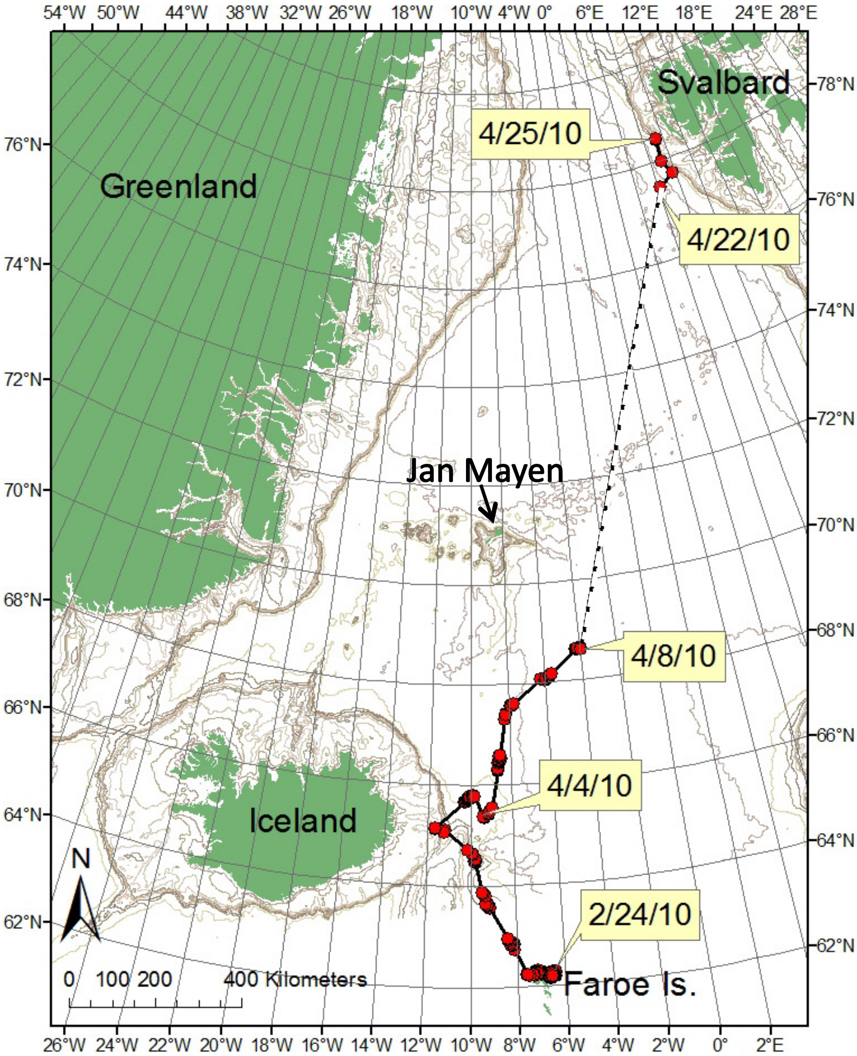
Data on haul-out activity and temperature were extracted from the Argos dispose files by use of the Wildlife Computers Argos Message Decoder software version 1.0.55. Haul-out was inferred from the activity of the SWS. We determined the percentage of time per hour and day that the walrus spent (1) on land, and (2) at the water's surface.

We defined haul-out to be when the SWS read ≥70% "dry" during a 60 min interval. The duration of a single haul-out period was defined as the time elapsed between the beginning and the end of a continuous series of "≥70% dry" intervals. "Extended" haul-out period was defined as a haul-out period that was ≥ 2 hours. All ≥70% dry intervals were subtracted from the total sum of 60 min periods. Subsequently, the percentage of time the walrus was at water's surface (i.e. % of time when SWS was dry <70%) was calculated.

When the walrus was determined to be hauling out from SWS activity data, actual haul-out behaviour was verified from external temperature data recorded by the SLTs during the period in question. Haul-outs on land had an average of 64.3% (range: 31.9–100%) of the temperature counts in the 6 h blocks in the upper two bins (> 8 °C) confirming that the walrus was hauling out.

We also compared the extended haul-out with the number of high quality satellite locations (primarily LC3 but in a few cases LC2) received during the same period. These locations were used to determine the exact geographic locations of haul-out sites and they were compared with sea ice and substrate charts.

***Fig. 4.*** *Route of an adult male Atlantic walrus. During 29 March – 22 April 2010 the walrus moved from the Faroe Islands to the Svalbard archipelago.*




**Genetic analyses**

The ca. 1 g skin biopsy taken from the walrus on the Faroe Islands was stored in a saturated NaCl solution and at minus 20°C until analysed in the laboratory of the Department of Bioscience (Aarhus University, Denmark) in September 2011.

The data set for assignment was based on 14 nuclear markers (a subset of the 17 used by Andersen et al. 2014). The baseline populations consisted of 183 Atlantic walruses sampled in East Greenland during 2002–2010 and 66 sampled at Svalbard during 1992–93 and 2003 (Greenland Institute of Natural Resources and Norwegian Polar Institute, unpublished data). The probability of identity based on the 14 loci was estimated in Gimlet v1.3.3 (Valière 2003) and was low enough to discriminate individuals (PI(unbiased)= 2.893e-12, PI(sibs)= 2.684e-05) .

Population assignment was conducted using the assignment tests implemented in GENECLASS2 (Piry et al. 2004), which use the individual's multilocus genotype likelihoods to identify population origin (Paetkau et al. 2004). We used the frequency-based method (Paetkau et al. 1995) to calculate individual likelihood of belonging to a certain subpopulation. This method calculates the allele frequencies for each allele and estimates the likelihood of a diploid genotype to occur in the population according to Hardy-Weinberg proportions. The method assumes loci to accord to the Hardy-Weinberg expectations and linkage equilibrium, and that the observed allele frequencies are close to the exact frequencies in the population. The exclusion probability (at the 5% level) of a population as origin and the probability of an individual to be a migrant were calculated based on the re-sampling algorithm by Paetkau et al. (2004).

## RESULTS

**General weather conditions**

Between 22 February and 29 March 2010 (i.e. the period when the walrus was at the Faroe Islands) the weather was relatively cold and variable with typical conditions for this time of the year (cf. Cappelen and Laursen 1998) with night (03 local h)/day (15 h local h) mean temperatures at 4–5 °C and mean wind speeds at 33–39 km/h. The mean wind-chill index averaged -0.7 °C and 0.5 °C at 03 and 15 local hours, respectively (Table 1). Prevailing winds came from SW–W–NW. During 22 February and 29 March nine days had rain, which is less than average during this time of the year (cf. Cappelen and Laursen 1998). During 27–29 March, the period just before the walrus left the Faroe Islands, strong winds came from N/NE (mean wind speed: 79 km/h, sd=17.3, range: 44-105 km/h, n=10). During this period the wind chill index averaged -6.6 °C (sd=1.3, range: -4.5 to -8.0 °C, n=10).

**Movement**

Between 24 February and 29 March 2010 the walrus only made local movements, remaining in the fjords or very close to the coast of the Faroe Islands (< ca. 3 km offshore; Fig. 1). All at-sea locations were received from areas where water depths are <100 m. During this period total daily displacement did not exceed 9.8 km (maximum movement speed 0.24 km/h).

While in the eastern parts of the Faroe Islands the walrus occurred in Árnafjørður, southern Hvannasund, Borðoyarvík at the town of Klaksvík, and Gøtuvík. During the latter part of its stay it transmitted from the northern part of Sundalagið (i.e. the strait between Eysturoy and Streymoy) until the morning of 29 March when it commenced the journey north, making a short visit into the bay of Saksun (island of Streymoy) before leaving the Faroe Islands about noon (Fig. 1). The walrus headed in a northwest direction over the Iceland–Faroe Ridge towards Northeast Iceland (Fig. 4). On 2 April when at ca. 65° 08′ N and ca. 11° 41′ W, the animal then took a more or less straight course north-northeast. After 8 April no positions were received until 22 April 2010. The walrus apparently took a long swim over deep waters (>1000 m depths) until it reached the

**Table 1**: General weather conditions at the Faroe Islands recorded at Klaksvík during 22 February–29 March 2010 when an adult male walrus visited the islands.

| | Temperature | | Wind force | | Wind chill index | | Pressure | |
|---|---|---|---|---|---|---|---|---|
| | (°C) | (°C) | (km/h) | (km/h) | (°C) | (°C) | (hPa) | (hPa) |
| Local Time | 3 | 15 | 3 | 15 | 3 | 15 | 3 | 15 |
| Mean | 4.1 | 5.0 | 32.6 | 39.2 | -0.7 | 0.5 | 1006.8 | 1007.2 |
| SD | 3.2 | 3.4 | 16.4 | 21.8 | 4.0 | 4.9 | 11.6 | 11.5 |
| Range: | -2.9 – 8.5 | -3.0 – 9.6 | 0.8 – 69 | 0.4 – 113 | -8.5 – 6.3 | -10.5 – 10.1 | 976 –1027 | 992 –1027 |
| N | 36 | 36 | 36 | 36 | 36 | 36 | 36 | 36 |

western edge of the continental shelf of Svalbard, where it reached the sea ice for the first time since leaving the Faroe Islands and hauled out to rest (Fig. 5).

The walrus swam a minimum of 2,216 linear km between departure from the Faroe Islands on 29 March and the first haul-out on the sea ice at Svalbard on 22 April. Between 29 March and 8 April average swimming speed was ca. 4.8 km/h (1,162 km/14,482 min) using methods I and 4.5 km/h (sd=0.99, range: 2.6–6.5 km/h, n=10 24 h periods) or 108 km/24 h (range: 62–156 km/24 h) using method II. After the walrus reached the Svalbard continental shelf on 22 April until last location received on 25 April the movement rate slowed down considerably, and averaged 1.76 km/h (sd=0.04, range: 1.72–1.80 km/h, n=8), or 42 km/24 h.

**Haul-out, at-surface and feeding activity**

*At the Faroe Islands*

Activity data were available for 13 days during the period the walrus was at the Faroe Islands between 24 February and 29 March. The walrus hauled out on all days with the exception of 4 March, the only rainy day of the 13 days with activity data.

The activity recorded by the system indicated that the walrus used at least three sites for hauling out on land. It hauled out on the beach at the town of Árnafjørður at 62° 15′ N/06° 32′ W several times between 24 February and 1 March and hauled out three times between 2–4 March at Norðaritangi (62° 11′ N/06° 27′ W) on the eastern coast of Borðoy. After the new transmitter was deployed, the walrus hauled out several times at Ljósá (62° 16′ N/07° 03′ W) in Sundalagið from 26 March until it left the Faroe Islands (Fig. 1).

Individual haul-out periods (i.e. unaborted series of ≥70% dry SWS messages) lasted between 1 and 19 h (n=15). Duration of extended haul-out sessions (≥2 h) on land averaged 6.1 h (sd=5.1, range: 2–19 h, n=12). In total the walrus hauled out for an average of 24.4% of the time (sd=17.1, range: 0–58.3% per 24 h, n=13 d of monitoring of activity) and generally preferred to rest on land between ca. 22:00 and ca. 13:00 h local time with a peak around 2:00 h (Fig. 6). At this time of the year it is dark at the Faroe Islands between ca. 16 and ca. 08 h. When at sea the walrus spent ca. 9.3% of the time (% per h) at the water´s surface (sd=16.1%, n=198 h with records).

*After departure from the Faroe Islands*

After the walrus left the Faroe Islands on 29 March data on haul-out and at surface activity were available for 12 days until 24 April. Between leaving the Faroe Island and arriving to the Svalbard area (on 22 April) the walrus did not haul out. During this periods, 7.1% of the time was spent at the water´s surface (sd=7.1, n=251 h). After arriving in Svalbard 5 haul-out sessions were recorded on 22 and 24 April when the animal was in the vicinity of sea ice at ca. 77° 29′ N/08° 17′ E and at ca. 78° N/09° 1′ E, respectively, some 100 km west of the island of Spitsbergen. During late April this area had 1/10–7/10 cover of drift ice (Fig. 5).

On the two days with activity data from Svalbard the walrus hauled out for 38% and 93% of the time, respectively, and generally preferred to rest on ice between ca. 9:00 and ca. 19:00 h (Fig. 6). At this time of the year daylight exists for 24 h in the Svalbard area. Extended haul-outs lasted 9.7 h on average (sd=9.9, range: 3-21 h, n=3) during this time.

**Genetics**

Prior to assignment of the walrus from the Faroe Islands to subpopulation the genetic differentiation between the two baseline population samples (East Greenland and Svalbard–Franz Josef Land) was analysed using pair-wise FST-test (Goudet 1995). The result FST=0.041 (95% CI: 0.018–0.074) suggested that the two subpopulations were significantly different. The result of the assignment analysis showed that the probability of the Faroese walrus belonging to the East

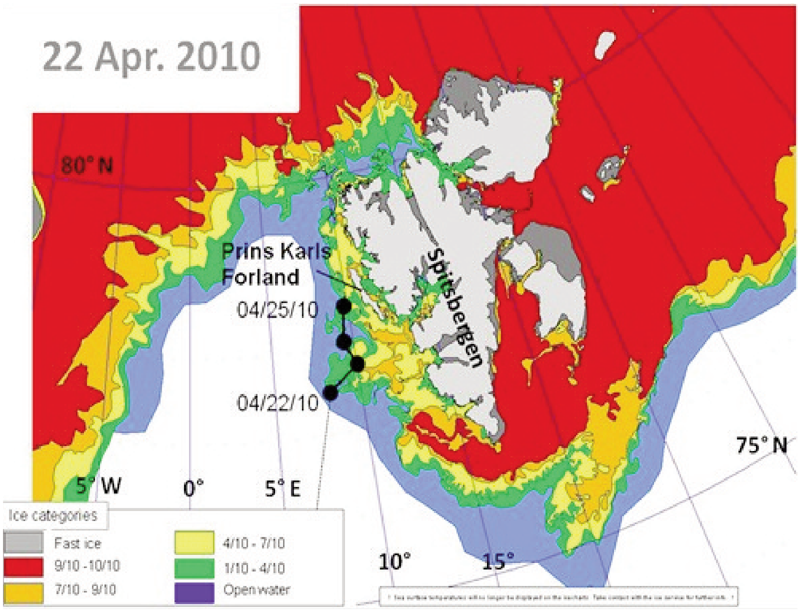



*Fig: 5. Ice conditions around the Svalbard archipelago on 22 April 2010 with the last locations (22–25 April 2010) received from an adult male Atlantic walrus tagged in the Faroe Islands. Ice source: Norwegian Sea Ice Service (Tromsø, Norway; www.met.no). Sea ice concentration categories are given in tenths.*

Greenland subpopulation was 0.073 whereas the probability of it belonging to the Svalbard–Franz Josef Land subpopulation was almost 10 times higher ($p=0.671$).

## DISCUSSION

**Timing and origin**

Despite a marked tendency of site tenacity in Atlantic walruses (e.g. Wiig et al. 1996, Born et al. 2005, Freitas et al. 2009), they are apparently in a process of expanding their range at Svalbard, East Greenland, and in the White Sea after depletion by hunting in the 20th century (Popov et al. 1990, Gjertz and Wiig 1994, Born et al. 1997). Both the East Greenland and the Svalbard–Franz Josef Land populations of walruses have shown signs of recovery and range expansion during the last several decades (Gjertz and Wiig 1994, Born et al. 1997, Lydersen et al. 2008, NAMMCO 2010), which may result in an increased occurrence of walrus visitors in boreal parts of Europe.

The timing of visits by vagrant walruses may provide some information as to the origin of walruses visiting the Faroe Islands (and the northwestern European coasts). The walrus visited the Faroe Islands during February and March. Previous observations of walruses at the Faroe Islands have also been made during winter (December–April; Bloch et al. 2001). Brun et al. (1968) mentioned that most sightings of walrus visitors to Norway had been made during the period July–October, however Gjertz et al. (1993) summarized 53 observations of walruses along the Norwegian coast during 1967–1992 and found that most of these later observations were recorded in late winter (January–April) north of Vestfjorden (ca. 68° N). Five records of walruses along the Danish North Sea coast after 1900 (Born 1988, plus one observation in 1999 and 2010, respectively; Born unpublished) also indicate that visits of walruses to this part of Europe are most common in winter. In contrast, the last three observations of walrus at Iceland have been made in spring and summer time (July 2005, May 2008 and September 2010; www.selasetur.is).

The Svalbard–Franz Josef Land walrus subpopulation primarily winters in the southern and northeastern parts of the Svalbard archipelago, in the pack ice between Svalbard and Franz Josef Land, and at Franz Josef Land. This subpopulation summers near-shore at Svalbard and Franz

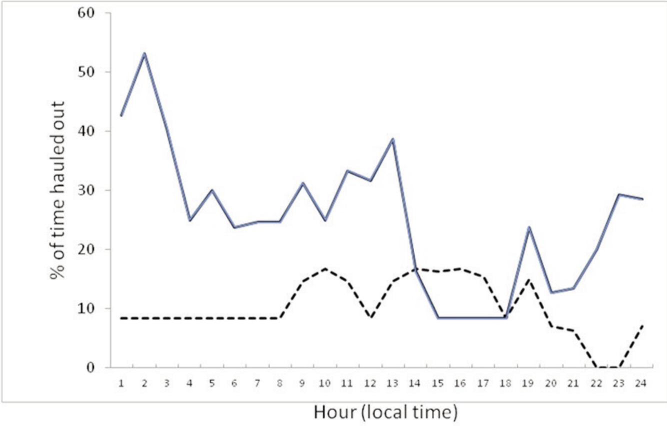



***Fig. 6**: Percentage of time (per 24 hour) that an adult male walrus hauled out at the Faroe Islands. The solid line shows fifteen haul-out sessions over thirteen days of during 24 February–5 March and 25–29 March 2010. The dashed line shows haulouts after the walrus had left the Faroe Islands (5 haul-outs over 12 days during 30 March and 24 April 2010).*

Josef Land (Born et al. 1995 and references therein, Wiig et al. 1996, Freitas et al. 2009).

The East Greenland walrus subpopulation has its primary distribution north of ca. 70° 30′ N – and in particular north of ca. 74° N (Born and Knutsen 1992, Born et al. 1997, Born et al. 2005). Although some walruses may winter in small polynyas and in the shear zone between fast ice and pack ice south of the Northeast Water Polynya (NEW) the majority of walrus in East Greenland winter in the NEW north of ca. 79° N (Ibid.). During summer there is a gradual and inconspicuous migration of in particular male walruses south along the coast of East Greenland to their inshore summering areas (Ibid.). The timing of the subsistence catch of walrus in the two East Greenland hunting communities (Ittoqqortoormiit/Scoresbysund at ca. 70° 30′ N and Tasiilaq/Ammassalik at ca. 64° to ca. 68° N) reflects this migration pattern. Few walruses are only occasionally caught in the Tasiilaq/Ammassalik area. The seasonal distribution of catches in this area shows a clear peak in June–November (Born et al. 1997, Born 2009). It is therefore not very likely that walruses that visit the Faroe Islands and mainland Europe during winter have arrived from East Greenland. It is however plausible that walruses that visit Iceland during summer are migrants from close by East Greenland.

The significant genetic difference between samples from the East Greenland and Svalbard–Franz Josef Land subpopulations confirmed earlier findings based on a smaller dataset reported by Andersen et al. (1998). Although it was not possible to exclude at the 5% significance level that the Faroese walrus belonged to the East Greenland subpopulation, the probability that it did was low. Thus it was indicated that the Faroese walrus was a visitor from the Svalbard–Franz Josef Land subpopulation.

The Kara Sea–Southern Barents Sea–Novaya Zemlya walrus subpopulation occurs closest to the European coasts. This subpopulation has its western limit in the northern part of the White Sea and on the Murmansk coast at ca. 40° W, not far from Norway (Born et al. 1995, NAMMCO 2005). Walruses winter in the White Sea area (Born et al. 1995 and references therein). The regular occurrence of walruses in the White Sea perhaps reflects the inclination of walruses to return to their former habitat in these areas (Popov et al. 1990) and an increase in numbers (Ibid., Haug and Nilssen 1995). However, to our knowledge the specific movement patterns and the genetics of the Kara Sea–Southern Barents Sea–Novaya Zemlya subpopulation have never been studied. Hence, it has not been determined whether they are genetically different from other walrus subpopulations in the NE Atlantic. Consequently it cannot be determined if the walrus in this study eventually came from the White Sea area but it returned to the range of the Svalbard–Franz Josef Land subpopulation.

It has been speculated whether an apparent increase in occurrence of vagrant walruses in European waters is related to climate change or increase in populations in neighbouring areas (Born 1988). It might be assumed that walrus visits increase during cold periods with expansion of Arctic sea ice. However, since 1979 the sea ice in the Northeast Atlantic has decreased markedly (Divine and Dick 2006, Perovich and Richter-Menge 2009). During the period when walruses visit Europe (i.e. December–April) the sea ice in East Greenland (i.e. the Denmark Strait, Greenland Sea and Fram Strait) and the Barents Sea region has decreased with an average of 10–11%/decade during 1979–2006 (Perovich and Richter-Menge 2009).

**Sex and age**

The walrus at the Faroe Islands was an adult male. Most vagrant walruses are presumably males (Ritchie 1921, Brun et al. 1968, Mercer 1967, Gjertz et al. 1993, Gaard et al. 2006b, Anon. 2011b, Born unpubl. data). It is likely walrus males, and perhaps in particular subadult males, have a tendency to explore new areas. Among vagrants observed along the coasts of Norway since 1967 there has been a surplus of subadult males (Gjertz et al. 1993).

In several large mammal species there is a greater tendency for subadult males to have the greatest dispersal. Apparently, subadult mammalian males tend to be both relatively exploratory and risk prone (e.g. Greenwood 1980; Shrader and Owen-Smith 2002; Ferreras et al. 2004, Mares et al. 2008).

**Swimming speed**

While in the vicinity of the Faroe Islands the walrus moved locally with an average speed of ca. 0.2 km/h. This together with observations of faeces on the beach indicated the walrus was feeding in near shore shallow waters. During the journey north, the walrus swam with an average speed of ca. 4.5 km/h. This is very similar to mean swimming speed of 4.0 km/h (sd=4.0, min.–max.: 0.3–16.7 km/h) reported for travelling adult male walruses equipped with satellite transmitters in Northeast Greenland (Born and Knutsen 1992, Born et al. 2005).

**Haul-out and at-surface activity**

While at the Faroe Islands the walrus hauled out for ca. 24% of the time with no apparent diurnal variation in haul-out rhythm. However, caution must be taken when interpreting the activity statistics. Data on haul-out activity were only available for 13 days with a 20 days hiatus in the data series between 5 and 24 March. Nevertheless, the percentage of total time hauling out is in agreement with information on haul-out of walruses in the Arctic. Estimates of mean fraction of time spent out of the water by walruses during summer range from one quarter to one third of the time hauled out (Hills 1992, Born and Knutsen 1997, Born et al. 2005, Acquarone et al. 2006, Born and Acquarone 2007, Jay et al. 2001, Lydersen et al. 2008). However, these studies showed considerable individual variation in haul-out activity, which was also the case in a study of four subadult walruses in captivity (Pryaslova et al. 2009). Nevertheless, the fact that the adult male walrus at the Faroe Islands, even when experiencing different environmental conditions than in the Arctic, maintained the need to rest for ca. 24% of the time indicates that resting time in walruses to a large extent is governed by basic physiological requirements.

At the Faroe Islands haul-out bouts on land lasted an average of ca. 6 hours. This is shorter than that reported for walruses hauling out during summer at higher latitudes (e.g. Northeast Greenland, mean: ca. 38 h; Born and Knutsen 1997. Svalbard, mean: ca. 30 hours; Lydersen et al. 2008).

The walrus at the Faroe Islands rested on land between 22–13 local time with a peak during night. Several studies indicate that in the Arctic summer walruses prefer to haul out during afternoon and evening (e.g. Salter 1979, Born and Knutsen 1997). Generally the diurnal haul-out pattern is influenced by weather conditions and is in particular negatively affected by wind chill and precipitation (Ibid.). However, Lydersen et al. (2008) neither found a clear diurnal pattern in haul-out rhythm during summer at Svalbard nor any effect of wind chill on the tendency to haul out. Similarly we were not able to detect any significant relationship between haul-out and wind chill/barometric pressure/time of day or location (data not shown). The tendency for the Faroe walrus to haul out during night may simply reflect that during night there was reduced disturbance from local residents who came to see the animal—sometimes at close range. Furthermore, the relative short duration of haul-out bouts may also reflect disturbance.

When the Faroese walrus was at sea it spent 7–9% of the time at the surface. Surface times in walrus vary substantially among studies, however the estimate reported here is less than reported in other studies noting travelling and feeding walruses are at the surface for 11 to 24% of the time (Fay 1982, Born and Knutsen 1997 and references therein). Fay et al. (1997) summarized information on at surface time and found that walruses on average spend ca. 16% of the time at the surface during various behaviours. Studies involving time-depth recorders (TDR) and satellite linked dive recorders (SLDR) have estimated that walruses use ca. 25% to ca. 40% of their in water time between 0 and 2 m depth (Wiig et al. 1993, Jay et al. 2001, Gjertz et al. 2001). However, at surface estimates from studies involving tag attachments of SLDR and TDRs are influenced by factors like individual behaviour, tag programming, and perhaps most importantly the position of the tag on the animal. The position of the two tags on the body of the Faroe walrus and its behaviour likely explain why its "at surface time" was at the lower range of other estimates, as true surface time was probably underestimated.

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## REFERENCES

Acquarone M, Born EW and Speakman J (2006) Walrus (*Odobenus rosmarus*) field metabolic rate measured by the doubly labeled water method. *Aquat. Mamm.* 32(3):363–369. doi: http://dx.doi.org/10.1578/AM.32.3.2006.363

Andersen LW, Born EW, Gjertz I, Wiig Ø, Holm LE and Bendixen C (1998) Population structure and gene flow of the Atlantic walrus (*Odobenus rosmarus rosmarus*) in the eastern Atlantic Arctic based on mitochondrial DNA and microsatellite variation. *Mol. Ecol.* 7(10):1323–1336. doi: http://dx.doi.org/10.1046/j.1365-294x.1998.00455.x

Andersen LW, Born EW, Stewart REA, Dietz R, Doidge DW and Lanthier C (2014) A genetic comparison of West Greenland and Baffin Island (Canada) walruses: Management implications. *NAMMCO Sci. Publications*. 9: 33–52. doi: http://dx.doi.org/10.7557/3.2610

Anonymous (2011a) *Mammals*. http://www.jenskjeld.info/UK_side/mammals.html

Anonymous (2011b) *Walrus in Holland*. http://pal.home.xs4all.nl/walrus.htm

Bloch D (ed.), Sneli J-A, Schiøtte T, Jensen KR, Wikander PB and Stokland Ø (2005) *The Marine Mollusca of the Faroes*. Føroya Fróðskaparfelag Supplementum 42: 190 pp.

Bloch D (1998) A review of marine mammals observed, caught or stranded over the last two centuries in Faroese waters. In: *The Shetland Sea Mammal Report, 1997*. Published by the Shetland Sea Mammal Group, August 1998. ISSN 1461-3581:15–37

Bloch D, Mikkelsen B and Ofstad LH (2001) Marine mammals in Faroese waters with special attention to the south-southeastern sector of the region. Unpublished report from the Museum of Natural History, Tórhavn, Faroe Islands, 26 pp.

Born EW (1988) *Hvalrosstrejfere i Europa* (Walrus stragglers in Europe). *Flora og Fauna* (Århus) 94:9–14. In Danish with English summary

Born EW (1992) *Odobenus rosmarus* Linnaeus, 1758. Walross. In: Duguy R and Robineau D (eds.). Band 6: Meeressäuger. Teil II: Robben - Pinnipedia. Handbuch der Säugetiere Europas. AULA -Verlag Wiesbaden, 269–299

Born EW (2009) Walrus *Odobenus rosmarus* In: Boertmann D, Mosbech A, Schiedek D and Johansen K (eds.). The western Greenland Sea. A preliminary strategic environmental impact assessment of hydro¬carbon activities in the KANUMAS East area. Report from the National Environmental Research Institute, Aarhus University, Denmark, 100–107. Available at: http://www2.dmu.dk/Pub/FR719.pdf

Born EW and Knutsen LØ (1992) Satellite-linked radio tracking of Atlantic walruses (*Odobenus rosmarus rosmarus*) in northeastern Greenland, 1989–1991. *Z. Säugetierk*. 57:275–287

Born EW and Knutsen LØ (1997) Haul-out activity of male Atlantic walruses (*Odobenus rosmarus rosmarus*) in northeastern Greenland. *J. Zool. (Lond.)* 243(2):381–396. doi: http://dx.doi.org/10.1111/j.1469-7998.1997.tb02789.x

Born EW and Acquarone M (2007) An estimation of walrus predation on bivalves in the Young Sound area (NE Greenland). In: Rysgaard S and Glud RN (eds.). Carbon cycling in Arctic marine ecosystems: Case study Young Sound. *Medd. Grønland Biosci*. 58:176–191

Born EW, Heide-Jørgensen MP and Davis RA (1994) The Atlantic walrus (*Odobenus rosmarus rosmarus*) in West Greenland. *Medd. Grønland Biosci*. 40:1–33

Born EW, Gjertz I and Reeves RR (1995) Population Assessment of Atlantic Walrus. *Norsk Polarins. Medd*. 138:1–100

Born EW, Dietz R, Heide-Jørgensen MP and Knutsen LØ (1997) Historical and present status of the Atlantic walrus (*Odobenus rosmarus rosmarus*) in eastern Greenland. *Medd. Grønland Biosci*. 46:1–73

Born EW, Andersen LW, Gjertz I and Wiig Ø (2001) A review of genetic relationships of Atlantic walruses (*Odobenus rosmarus rosmarus*) east and west of Greenland. *Polar Biol*. 24(10):713–718. doi: http://dx.doi.org/10.1007/s003000100277

Born EW, Rysgaard S, Ehlmé G, Sejr M, Acquarone M and Levermann N (2003) Underwater observations of foraging free-living walruses (*Odobenus rosmarus*) including estimates of their food consumption. *Polar Biol*. 26:348–357. doi: http://dx.doi.org/10.1007/s00300-003-0486-z

Born EW, Acquarone M, Knutsen LØ and Toudal L (2005) Homing behaviour in an Atlantic walrus (*Odobenus rosmarus rosmarus*). *Aquat. Mamm*. 31:23–33. doi: http://dx.doi.org/10.1578/AM.31.1.2005.23

Brun E, Lid G, and Lund HMK (1968) *Hvalros*, Odobenus rosmarus, *på norskekysten* (Walruses along the Norwegian coast). Fauna (Oslo) 21:7–20. In Norwegian

Cappelen J and Vaarby Laursen E (1998) The Climate of the Faroe Islands - with climatological standard normals, 1961-1990. Danish Meteorological Institute Technical Report, 98-14:1–62

Dietz R, Born EW, Stewart REA, Heide-Jørgensen MP, Stern H, Rigét F, Toudal L, Lanthier C, Villum Jensen M, and Teilmann J (2014) Movements of walruses (*Odobenus rosmarus*) between Central West Greenland and Southeastern Baffin Island, 2005–2008. *NAMMCO Sci. Publ*. doi: http://dx.doi.org/10.7557/3.2605

Divine DV and Dick C (2006) Historical variability of sea ice edge position in the Nordic seas. *J. Geophys. Res*. Vol III, C01001. doi: http://dx.doi.org/10.1029/2004JC002851

Douglas D (2006) The Douglas Argos-Filter Algorithm, Version 7.03. U.S. Geological Survey, Anchorage, Alaska

Fay FH (1982) Ecology and Biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North American Fauna No. 74. U.S. Department of the Interior Fish and Wildlife Service, 279 pp.

Fay FH, Eberhardt LL, Kelly BP, Burns JJ and Quakenbush LT (1997) Status of the Pacific walrus population, 1950-1989. *Mar. Mamm. Sci*. 13(4):537–565. doi: http://dx.doi.org/10.1111/j.1748-7692.1997.tb00083.x

Ferreras P, Delibes M, Palomares F, Fedriani JM, Calzada J, and Revilla E (2004) Proximate and ultimate causes of dispersal in the Iberian lynx *Lynx pardinus*. *Behav. Ecol*. 15(1):31–40. doi: http://dx.doi.org/10.1093/beheco/arg097

Freitas C, Kovacs KM, Ims RA, Fedak M and Lydersen C (2009) Deep into the ice: over-wintering and habitat selection in Atlantic walruses. *Mar. Ecol. Prog. Ser*. 375: 247–261. doi: http://dx.doi.org/10.3354/meps07725

Gaard E, Hansen B, Arge Jacobsen J, Magnussen E, Mikkelsen B, Olsen B, Steingrund P, and Sørensen J (2006a) *Havið kring Føroyar* (The Sea around the Faroe Islands). In: Fosaa AM, Gaard E, and Dalsgarð J (eds.) *Føroya náttúra – Livsfrøðiligt margfeldi* (The Nature and Biodiversity of the Faroe Islands). Føroya Skúlabókagrunnur, Tórshavn, 38–69. In Faroese

Gaard E, Reinert A, Reinert J and Sørensen J (2006b) *Firðir og sund* (Fjords and Sounds). In: Fosaa AM, Gaard E and Dalsgarð J (eds.) *Føroya náttúra – Livsfrøðiligt margfeldi* (The Nature and Biodiversity of the Faroe Islands). Føroya Skúlabókagrunnur, Tórshavn, 72–89. In Faroese

Gjertz I and Wiig Ø (1994) Past and present distribution of walruses in Svalbard. *Arctic* 47(1):34–42. URL: http://www.jstor.org/stable/40511527

Gjertz I, Henriksen G, Øritsland T and Wiig Ø (1993) Observations of walruses along the Norwegian coast 1969-1992. *Polar Res*. 12(1):27–31. doi: http://dx.doi.org/10.1111/j.1751-8369.1993.tb00419.x

Gjertz I, Griffiths D, Krafft BA, Lydersen C and Wiig Ø (2001) Diving and haul-out patterns of walruses *Odobenus rosmarus* on Svalbard. *Polar Biol*. 24(5):314–319. doi: http://dx.doi.org/10.1007/s003000000211

Goudet J (1995) FSTAT 2.9.3.1: A computer program to calculate F statistics. *J. Hered*. 86:485–486.

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav*. 28:1140–1162. doi: http://dx.doi.org/10.1016/S0003-3472(80)80103-5

Haug T and Nilssen KT (1995) Observations of walrus (*Odobenus rosmarus rosmarus*) in the southeastern Barents and Pechora seas in February 1993. *Polar Res*. 14(1):83–86. doi: http://dx-doi.org/10.1111/j.1751-8369.1995.tb00712.x

Hills S (1992) The effect of spatial and temporal variability on population assessment of Pacific walruses. [PhD-thesis]. University of Maine, Orono, USA, 120 pp.

Jay CV, Farley SD and Garner GW (2001) Summer diving behaviour of male walruses in Bristol Bay, Alaska. *Mar. Mamm. Sci*. 17(3):617–631. doi: http://dx.doi.org/10.1111/j.1748-7692.2001.tb01008.x

Jensen AS (1927) Small contributions to our knowledge of the Danish fauna 4. On a walrus (*Trichechus rosmarus L*.) which has visited Denmark and probably four other European countries. *Vid. Medd. Dansk Naturhist*. For. 84:189–193

Kingsley MCK (1998) Walruses, *Odobenus rosmarus*, in the Gulf and Estuary of the St. Lawrence, 1992–1996. *Can. Field Nat*. 112(1):90–93

Kristjánsson L (1986) *Íslenzkir Sjávarhættir* Vol. V (“Icelandic Maritime Customs”). *Bókaútgáfa Menningarsjóðs*, Rekjavik, Iceland, 108–110. (*fide* Pierce 2009). In Icelandic

Lydersen C, Aars J and Kovacs KM (2008) Estimating the number of walruses in Svalbard from aerial surveys and behavioural data from satellite telemetry. *Arctic* 61(2):119–128. URL: http://www.jstor.org/stable/40513198

Mares R, Moreno RS, Kays RW and Wikelski M (2008) Predispersal home range shift of an ocelot *Leopardus pardalis* (Carnivora: Felidae) on Barro Colorado Island, Panama. *Rev. Biol. Trop*. 56:779–787

Mercer MC (1967) Records of the Atlantic walrus, *Odobenus rosmarus rosmarus*, from Newfoundland. *J. Fish. Res. Bd. Can.* 24(12):2631–2635. doi: http://dx.doi.org/10.1139/f67-213

NAMMCO — North Atlantic Marine Mammal Commission (2005) Annex 3. Report of the Scientific Committee Working Group on stock status of walrus in the North Atlantic and adjacent seas. In: NAMMCO Annual Report 2005, North Atlantic Marine Mammal Commission, Tromsø, Norway, 279–308. http://www.nammco.no/webcronize/images/Nammco/806.pdf

NAMMCO — North Atlantic Marine Mammal Commission. (2010) Annex 2. Report of the NAMMCO Scientific Working Group on walrus. In: NAMMCO Annual Report 2010, North Atlantic Marine Mammal Commission, Tromsø, Norway, 333–358. http://www.nammco.no/webcronize/images/Nammco/955.pdf

Nores C and Pèrez C (1988) The occurrence of walrus (*Odobenus rosmarus*) in southern Europe. *J. Zool. (Lond.)* 216(4):593–596. doi: http://dx.doi.org/10.1111/j.1469-7998.1988.tb02457.x

Paetkau D, Calvert W, Stirling I and Strobeck C (1995) Microsatellite analysis of population structure in Canadian polar bears. *Mol. Ecol.* 4(3):347–354. doi: http://dx.doi.org/10.1111/j.1365-294X.1995.tb00227.x

Paetkau D, Slade R, Burdens M and Estoup A (2004) Genetic assignment methods for direct, real-time estimation of migration rates: a simulation-based exploration of accuracy and power. *Mol. Ecol.* 13(1):55–65. doi: http://dx.doi.org/10.1046/j.1365-294X.2004.02008.x

Perovich DK and Richter-Menge JA (2009) Loss of ice in the Arctic. *Ann. Rev. Mar. Sci.* 1:417–441. doi: http://dx.doi.org/10.1146/annurev.marine.010908.163805

Petersen Æ (1993) *Rostungar við Ísland að fornu og nýju* (Walruses at Iceland in past and recent times). In: Hersteinsson, P. and Sigbjarnarson, G. (eds.). *Villt Islensk spendýr* (Wild mammals of Iceland). *Hið Íslenska Náttúrfræðifélag*, Reykjavik, Iceland, 214–216. In Icelandic

Pierce E (2009) Walrus hunting and the ivory trade in early Iceland. *Archaeol. Islandica* 7:55–63

Piry S, Alapetite A, Cornuet J-M, Paetkau D, Baudouin L and Estoup A (2004) GeneClass2: A software for genetic assignment and first generation migrants detection. *J. Hered.* 95:536–539. doi: http://dx.doi.org/10.1093/jhered/esh074

Popov L, Timoshenko Iu and Wiig Ø (1990) Review of history and present status of world walrus stocks: Barents, Kara and White Seas. In: Fay FH, Kelly BP and Fay BA (eds.) The Ecology and management of Walrus Populations. Report of an international workshop 26-30 March 1990, Seattle, Washington, USA. Marine Mammal Commission Report PB91-100479, 6-14

Pryaslova JP, Lyamin OI, Siegel JM and Mukhametov LM (2009). Behavioral sleep in the walrus. *Behav. Brain Res.* 201:80–87. doi: http://dx.doi.org/10.1016/j.bbr.2009.01.033

Ritchie J (1921) The walrus in British waters. *The Scottish Naturalist* 5–9:77–86

Salter R (1979) Site utilization, activity budgets and disturbance responses of Atlantic walruses during terrestrial haul-out. *Can. J. Zool.* 57(6):1169–1180. doi: http://dx.doi.org/10.1139/z79-149

Shrader AM and Owen-Smith N (2002) The role of companionship in the dispersal of white rhinoceroses (*Ceratotherium simum*). *Behav. Ecol. Sociobiol.* 52(3):255–261. doi: http://dx.doi.org/10.1007/s00265-002-0506-y

Valière N (2003) GIMLET: a computer program for analysing genetic individual identification data. *Mol. Ecol. Notes.* 2(3):377–379. doi: http://dx.doi.org/10.1046/j.1471-8278.2002.00228.x

Van Bree PHJ (1997) On extralimital records of Arctic seals (Mammalia, Pinnipedia) on the Western European continental coast in the past and the present—a summary. *Beaufortia* 47:153–256

Wiig Ø, Gjertz I, Griffiths D and Lydersen C (1993) Diving patterns of an Atlantic walrus *Odobenus rosmarus rosmarus* near Svalbard. *Polar Biol.* 13(1):71–72. doi: http://dx.doi.org/10.1007/BF00236586

Wiig Ø, Gjertz I and Griffiths D (1996) Migration of walruses (*Odobenus rosmarus*) in the Svalbard and Franz Josef Land area. *J. Zool. (Lond.)* 238(4):769–784. doi: http://dx.doi.org/10.1111/j.1469-7998.1996.tb05429.x