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The predictable narwhal: satellite tracking shows behavioural similarities between isolated subpopulations

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Abstract

Comparison of behavioural similarities between subpopulations of species that have been isolated for a long time is important for understanding the general ecology of species that are under pressure from large-scale changes in habitats. Narwhals (*Monodon monoceros*) east and west of Greenland are examples of separated populations that, in different ocean parts, will be coping with similar anthropogenic and climate-driven habitat alterations. To study this, 28 narwhals from the Scoresby Sound fjord system were tracked by satellite in 2010–2013. The average duration of contact with the whales was 124 days with one tag lasting 305 days and one whale recaptured <1 km from its tagging site 366 days later. All whales exhibited the same migratory pattern. The whales departed from the summering grounds in Scoresby Sound in September and arrived at the edge of the continental shelf by November. Here, they stayed through May–June and conducted daily dives to the mesopelagic zone at ~1000 m depth. Despite the isolation by the landmass of Greenland and the genetic differentiation from other narwhal populations, there is still a remarkable similarity not just in behavioural traits like phenology of migrations and movements in relation to sea ice formation, but also in site fidelity, diving behaviour, feeding ecology, habitat selection, daily travel speed and even potential conflicts with fisheries for Greenland halibut (*Reinhardtius hippoglossoides*). Greenland halibut are likely target prey during the deep dives in winter but capelin (*Mallotus villosus*) may, with ocean warming, become of increasing importance. The ocean-wide predictability in culturally inherited migration patterns, size of wintering grounds and habitat selection among narwhal populations is certainly different from other Arctic cetaceans and renders narwhals more vulnerable to large-scale changes in their restricted and specialized habitats.

Introduction

Phenology and behavioural traits from isolated subpopulations of the same species may, depending on the period of separation, develop in different directions in response to the dynamics of their habitats. Studies of behavioural characteristics of spatially separated subpopulations provide insight into the speed of the behavioural changes the subpopulations are subject to, but may also offer information that is useful for understanding species-level responses to large-scale regional or global habitat changes affecting separate subpopulations (cf. Stewart *et al*., 2010). Changes in climate and associated changes in anthropogenic activities will likely affect animals at the species level leaving no or few subpopulations unaffected. Comparative studies of marine animals inhabiting isolated, but apparently similar environments are particularly useful for assessing population-level effects. One example of an animal with several isolated subpopulations in similar habitats is the narwhal (*Monodon monoceros*) that west of Greenland has at least five subpopulations (Heide-Jørgensen *et al*., 2012*a*) and east of Greenland exists in an unknown number of subpopulations. The eastern and western populations of narwhals in Greenland have been physically separated at least since the last glaciation (>10.000 years). In comparison, the closely related beluga whale (*Delphinapterus leucas*) that occurs in many isolated populations in the Arctic, shows a large diversity in behavioural traits pertaining to migratory habits, habitat selection and diving behaviour (e.g. O'Corry-Crowe, 2009).

The narwhal is the only odontocete that occurs year-round off East Greenland and in the Greenland Sea. Narwhals are known to occur from 64°N to about 82°N where they are primarily located along the ice edge in spring and in the fjords in East Greenland during the open-water season in August through October, but they are also seen and caught in all months in Southeast Greenland. The largest concentration of narwhals in East Greenland occurs in Scoresby Sound (Larsen *et al*., 1994; Heide-Jørgensen *et al*., 2010). The few offshore observations of narwhals in the Greenland Sea are primarily from ice-covered areas between Scoresby Sound and Svalbard (Dietz *et al*., 1994). The Greenland Sea provides a habitat similar to Baffin Bay where narwhals are known to occur in offshore areas in winter (Heide-Jørgensen *et al*., 2012*a*). Both areas are seasonally ice-covered, have deep-water basins with steep slopes along the continental shelf and include typical narwhal prey like polar cod (*Boreogadus saida*), Greenland halibut (*Reinhardtius hippoglossoides*) and squids (e.g. *Gonatus fabricii*). One hypothesis is that certain areas of the Greenland Sea, yet unknown, are used as wintering grounds for narwhals that occur in coastal areas (i.e. the fjords of East Greenland) during summer. A similar shift between coastal summering grounds during the open-water season and ice-covered wintering grounds has been observed for narwhals in Baffin Bay and adjacent areas (e.g. Heide-Jørgensen *et al*., 2003).

Genetic studies have been of limited use for identifying population delineations of narwhals because of low diversity observed in their mtDNA. Nevertheless, narwhals from East Greenland have been shown to be genetically distinct from Canadian and West Greenlandic narwhals (Palsbøll, Heide-Jørgensen & Dietz, 1997). This is in agreement with the long-term hiatus in distribution between narwhals east and west of Greenland. Most information on movement patterns of narwhals has been obtained through satellite telemetry studies in the eastern Canadian Arctic and in West Greenland (Heide-Jørgensen *et al*., 2002, 2012*a*; Dietz *et al*., 2008). Based on two decades of satellite tracking work with >100 instrumented whales, it has been proposed that narwhals in Baffin Bay and adjacent waters have a metapopulation structure with limited exchange between reproductively isolated subpopulations (Heide-Jørgensen *et al*., 2012*a*). These large-scale satellite tracking studies have also revealed that narwhals follow strict migratory schedules, have considerable site fidelity to certain coastal summering grounds and choose specific wintering grounds over deep water in the dense pack ice. Nothing is known about the movement patterns and wintering areas of narwhals in East Greenland and it is tempting to assume that they have similar strict migratory schedules as narwhals west of Greenland. Considering the long coastline of East Greenland with many summering localities suitable for narwhals, it is also likely that some metapopulation structure of narwhals persist in this area.

The study presented here uses satellite tracking to provide the first insight into the migratory patterns of the stock of narwhals that summer in Scoresby Sound. We show that not only are there many similarities in the migratory patterns, diving behaviour, migration phenology and habitats of east and west Greenland narwhals, but there is also a remarkable year-to-year predictability in these characteristics.

Materials and methods

Live-capturing operations were conducted from a field station at Hjørnedal inside Scoresby Sound in collaboration with Inuit hunters that use the area as a hunting ground (Fig. 1). Set nets of either 40 or 80 m length and 5 to 8 m deep were deployed from shore to an anchor at suitable sites. Lookouts for whales were maintained from land-based promontories, from which the nets were kept under constant surveillance. When whales were observed in the area, several 15- to 20-foot fiberglass boats were launched. As soon as there were indications of a whale being entangled, the net was released from the anchor and the whale was pulled to the surface and towards the shore. Duration of handling of captured whales was <30 min and was conducted near the shore by four persons in survival suits standing next to the whale while supporting it. Twenty-eight narwhals were instrumented with backpack satellite transmitters following instrumentation techniques used in similar studies in Canada and West Greenland (Heide-Jørgensen *et al*., 2003; Dietz *et al*., 2008). Sex of the whales was determined based on presence (male) or absence (female) of a tusk.

Three types of satellite transmitters, all manufactured by Wildlife Computers (Redmond, Seattle, WA, USA), were deployed on the narwhals (see Supporting Information).

Positions of the whales were obtained from the Argos satellite data processing system with Kalman filtering algorithm, and accuracy of locations was assessed by Argos location codes (LC) 3–0, A and B (CLS America, 2007). The Scoresby Sound area is a complex fjord system where filtering of positions is necessary to avoid positions on land (see Supporting Information). Daily average positions were calculated for all good-quality positions (LC > 0). If no good-quality positions were available, low-quality positions (LC = 0, A and B) were used. Mean distance travelled per hour was estimated using daily average positions every 48 h. Maps of narwhal movements were generated using ArcMap (10.2, ESRI, Redlands, CA, USA). Bathymetric contours based on 1° resolution data were obtained from the International Bathymetry Chart of the Arctic Ocean (IBCAO, Jakobsson *et al*., 2000). Narwhals travel close to shore and some positions from inside Scoresby Sound were apparently on land. However, both digitized coastlines and bathymetry of East Greenland are uncertain, and it was therefore decided to keep positions on land and only omit a few obvious erroneous positions >5 km from shore. The date of departure from Scoresby Sound was defined as the day the whales passed east of 22°W (Fig. 1). Arrival at the wintering ground was defined as the first time the whales went south of 69°N. The area usage during winter was defined for positions obtained during the period from the first day after passing 69°N to the 30 June. The Spatial Analyst extension (10.2) was used to generate a kernel density estimate, which was consequently mapped as a 50, 75 and 95% kernel home range. Daily movements were estimated based on the daily average positions (LC = 1–3) and distance travelled per time unit was estimated from consecutive positions obtained at intervals of 0.5 to 5 h.

In addition to providing positions, the satellite transmitters also used a pressure transducer to provide a maximum daily

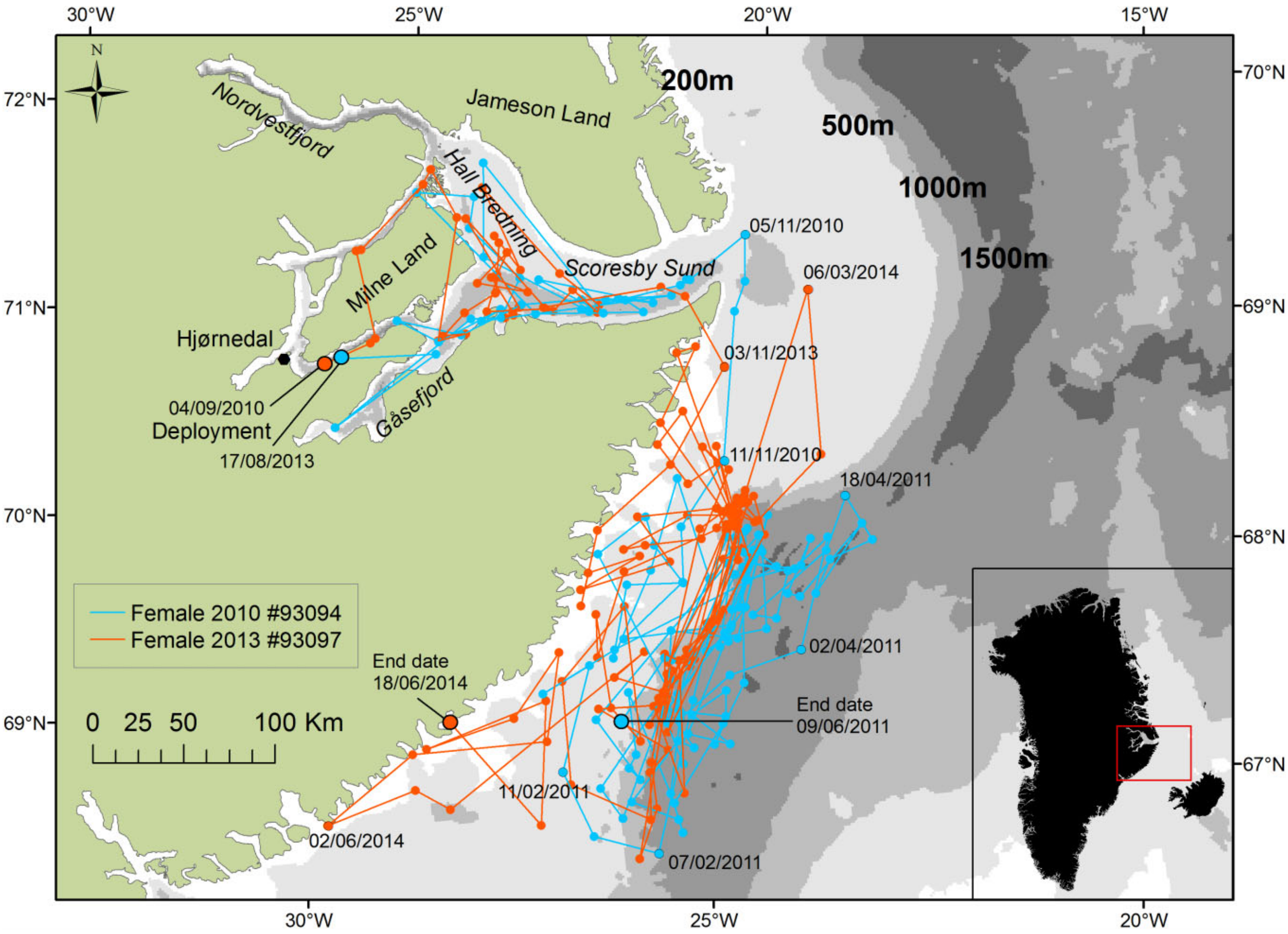

Figure 1 Example tracks of two narwhals tagged at Hjørnedal in August-September 2010 and 2013. These two whales had the longest satellite records.

diving depth for each animal. These data were extracted with Wildlife Computers' Data Analysis Program and compared with the bathymetry at each position. Three SPLASH tags gave 46 readings of max dives >2000 m, of which one tag made 42 of these readings. There were no maximum depth readings between 1592 m and >2000 m and the whales did presumably not visit areas with water depths exceeding 2000 m. Depth readings >2000 m were therefore considered erroneous and were not included in the analysis.

A stratified random bottom trawl survey for Greenland halibut was conducted in the narwhal habitat in the outer part of Scoresby Sound and offshore at the wintering grounds at depths down to 1500 m during 16 September–2 October 2006 (see Supporting Information).

Results

Seven narwhals were instrumented in each of 2010 and 2011, six in 2012 and 8 in 2013 (Table 1). The overall average from all tags was 13 positions of good quality per day. Out of a total of 1991 days with positions, 143 days (or 7%) had only low-quality positions. The 16 Mk10 and the three SPLASH tags provided on average 151 and 144 days with positions (all qualities), respectively. Two whales with Mk10 tags provided particularly long tracks into June the following year (Fig. 1) and one of the tags showed signs of battery exhaustion (voltage <3 V) after >33 000 transmissions. The Mk10A tags were allowed to make 500 transmissions per day and they showed signs of battery exhaustion with voltage dipping below 3V after 2 months in both years. The Mk10As deployed in 2013 had six wires attaching them to the animal instead of four, but it is not known if this explains why these tags provided, on average, twice as many days with positions in 2013 (77 days) compared with 2012 (39 days). Whale #3965 was tagged on 13 August 2013 and while its transmitter stopped on 15 December 2013, the whale was taken in a local hunt <1 km from the tagging site on 14 August 2014 with the tag still attached to four of the six nylon pin ends on the back of the whale (Fig. 2). The recapture confirmed that the attachment approach can potentially last for >1 year

Table 1 List of narwhals tagged in Scoresby Sound in 2010–2013

Transmitter	Date	Sex	Length (cm)	Tail width (cm)	Tusk (cm)	Last positions	Mean daily travel distance (km)	Mean travel distance 5–15 h (km/h)	Range of maximum depth of dives (m)	Date of departure from Scoresby Sound	Arrival in wintering area <69°N
#3960_2010[a]	2 Sep 2010	♂	400	120	90	29 Dec 2010	22	2.6	270–1086	3 Nov	7 Nov
#3962_2010[a]	2 Sep 2010	♂	355	77	89	4 Sep 2010	–	–	–	–	–
#3963_2010[a]	22 Aug 2010	♀	395	89	–	17 Feb 2011	22	2.7	270–1586	1 Nov	5 Nov
#3964_2010[a]	2 Sep 2010	♀	385	95	104	15 Feb 2011	19	1.7	314–1592	1 Nov	9 Nov
#6335_2010[a]	4 Sep 2010	♀[c]	395 (calf 225)	95 (calf 55)	–	7 Dec 2010	18	2.3	402–1116	30 Oct	7 Nov
#93093_2010[a]	4 Sep 2010	♂	275	69	9	13 Nov 2010	22	3.2	520–746	–	–
#93094_2010[a]	4 Sep 2010	♀	415	95	–	9 Jun 2011	19	2.3	270–1480	7 Nov	11 Nov
#6336_2011[a]	12 Aug 2011	♀	315	68	–	6 Mar 2012	24	1.6	282–914	18 Oct	26 Oct
#7926_2011[a]	12 Aug 2011	♂	407	104	100	9 Jan 2012	23	3.5	164–482	14 Oct	18 Oct
#10946_2011[a]	19 Aug 2011	♂	364	80	60	18 Mar 2012	23	1.0	326–1352	18 Oct	22 Oct
#20162_2011[a]	12 Aug 2011	♂	392	97	98	18 Jan 2012	24	1.8	384–924	12 Oct	22 Oct
#93095_2011[a]	16 Aug 2011	♂	370	90	83	22 Oct 2011	23	3.2	598–918	14 Oct	22 Oct
#93098_2011[a]	13 Aug 2011	♂	290	72	23	3 Mar 2012	19	1.7	320–754	12 Oct	22 Oct
#93101_2011[a]	19 Aug 2011	♂	453	108	170	12 May 2012	21	2.5	346–1576	22 Oct	24 Oct
#21791_2012[b]	23 Aug 2012	♂	440	110	150	10 Apr 2013	34	2.6	306–1504	8 Oct	31 Oct
#21792_2012[b]	19 Aug 2012	♀?	280	68	–	3 Dec 2012	29	1.5	376–822	12 Oct	31 Oct
#22849_2012[STP]	17 Aug 2012	♂	335	82	50	28 Sep 2012	39	2.9	562–762	–	–
#22850_2012[STP]	19 Aug 2012	♂	400	100	>65	3 Oct 2012	32	3.2	568–914	–	–
#22853_2012[STP]	18 Aug 2012	♂	278	66	28	22 Sep 2012	32	2.7	520–754	–	–
#24638_2012[STP]	19 Aug 2012	♀	400	98	–	21 Sep 2012	27	5.5	466–746	–	–
#3963_2013[STP]	17 Aug 2013	♂	400	96	106	5 Nov 2013	34	2.7	414–1444	2 Nov	–
#3964_2013[STP]	13 Aug 2013	♂	356	90	65	5 Nov 2013	31	2.0	446–1116	2 Nov	–
#3965_2013[STP]	13 Aug 2013	♀[d]	420	104	–	15 Dec 2013	30	–	162–1558	1 Nov	–
#6335_2013[STP]	17 Aug 2013	♂	390	85	82	18 Oct 2013	36	1.1	474–980	–	–
#20685_2013[b]	20 Aug 2013	♂	327	71	23	24 Nov 2013	19	3.2	156–854	2 Nov	20 Nov
#93096_2013[a]	8 Aug 2013	♀	420	90	–	2 Sept 2013	26	–	152–328	–	–
#93097_2013[a]	17 Aug 2013	♀	385	98	–	18 Jun 2014	18	4.1	121–1562	2 Nov	9 Nov
#93102_2013[a]	17 Aug 2013	♂	417	97	109	24 Oct 2013	20	0.1	212–990	–	–

Travel distance is calculated between average daily positions every 48 h. '?' in the table indicate uncertain determination.

[a] Mk10 tags.

[b] Splash tags.

[c] With calf.

[d] When recaptured in 2014 this tuskless whale was identified as a male based on its 15-cm-long testes.

[STP] Mk10A with stomach temperature pill.

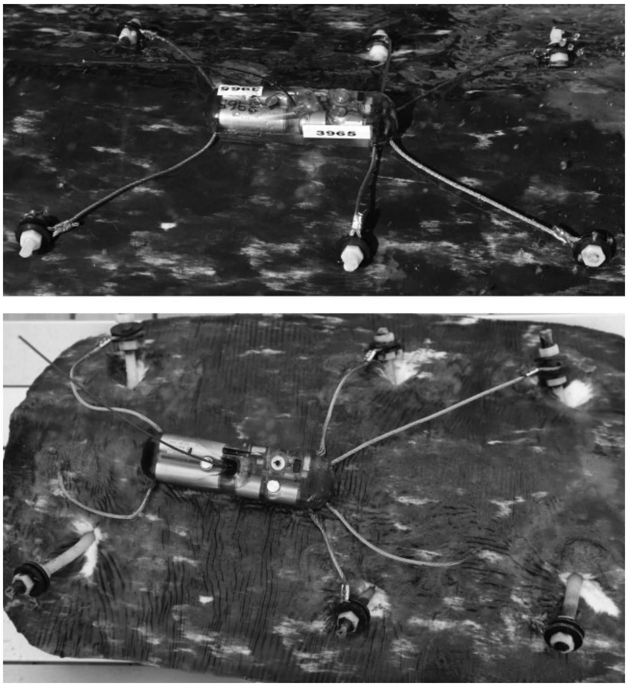

Figure 2 Narwhal #3965, tagged with a six-legged Mk10A tag on 13 August 2013 (top picture), was harvested by a local hunter on 14 August 2014 (bottom picture) within 1 km of the tagging site. The tag had moved about 2 cm backwards from its initial position and skin had overgrown the openings at the pins. Two wires (front and rear) on the right side were broken at the site of the thalorite attachment. The whale was identified as a female at the initial capture due to the absence of a tusk but during dissection after its recapture two 15-cm-long testes were found and no signs of female sex organs.

and that the tag failed because the batteries were exhausted (<1.2 V).

The 2011–2013 deployments were conducted 2–3 weeks earlier in the summer than the 2010 deployments, and offered more positions from the summer habitat in the inner parts of the fjord system (Fig. 3). The narwhals mainly used the channels around Milne Land and the two side-fjords Gåsefjord and Nordvestfjord (see Fig. 1). Several whales ventured up to the very end of Nordvestfjord close to the glacier outlet. Some side-fjords were for unknown reasons not visited by any of the 28 whales. In September, the narwhals began to spend time in Hall Bredning and the opening of Scoresby Sound, where they mainly used the deep southern parts and avoided the shallow coastal areas close to Jameson Land (Figs 1 and 3). In October, the inner parts of the fjord system around Milne Land were abandoned and the whales began to leave the fjord. The movement out of the fjord was also concentrated in the southern part of the entrance to Scoresby Sound at water depths ranging between 500 and 1000 m. The average departure day from Scoresby Sound was 24 October, with some variation: 10 October in 2012, 15 October in 2011 and 2 November in 2010 and 2013. The whales went straight to the wintering ground south of 69°N, off the Blosseville Coast where they on average arrived 10 days (range: 1–9 November) after they had departed Scoresby Sound. In November, the whales were primarily found on the East Greenland shelf area at water depths >500 m. From December through February they moved increasingly further offshore, but were rarely more than 100 km off the coast. They swam along the continental slope, which over a short distance dropped from 500 to 1500 m (Fig. 4). In March through May, they were primarily found over deep water from 1000 to 1500 m. The 95% kernel-based winter area usage estimate for all whales and all years was 34 581 km^2 for the period 1 December through 31 March (Fig. 4).

Two whales were tracked for >10 months (until June the following year, Fig. 1). One was still on the wintering ground when contact was lost and the other was visiting coastal areas while heading north towards Scoresby Sound. However, evidence for site fidelity to the summering ground was obtained from one whale that was recaptured at the tagging locality 366 days after it was tagged (Fig. 2). Local hunters took the whale from a group where four other individuals were captured live for tagging.

The mean daily travel distance for the 27 whales with more than 2 days of tracking was 25 km day^{-1} (SD 6.1). This corresponds to an average distance of 1.1 km h^{-1} (SD 0.25, Table 1). The mean daily travel distance declined from 27 km day^{-1} (SD 19.9) inside Scoresby Sound and during the fall migration to the wintering ground, to 21 km day^{-1} (SD 14.2) on the wintering ground south of 69°N. Females ($n = 8$) travelled a significantly shorter distance per day than males ($n = 18$, ANCOVA with day as covariate, $P < 0.001$, mean = 27 km day^{-1} for males and 22 km day^{-1} for females) with one female with a calf (#6335) travelling the shortest distance (18 km day^{-1}). However, the travel distance evaluated for consecutive positions separated by 0.5–5 h (mean 4.3 km h^{-1}, SD 0.6) or 5–15 hs (mean 2.5 km h^{-1}, SD 1.1) did not vary between sexes. The travelling distance of the whales was significantly higher in June (mean = 9.9 km h^{-1}, *t*-test $P < 0.0001$) compared with all other months (mean 4.2 km h^{-1}).

When the whales were in the inner part of the fjords in August, the maximum daily diving depth (as measured every other day; see Table 1) was usually less than 800 m (mean 615 m, SD 185, Fig. 5). In Hall Bredning and Scoresby Sound, the average increased to 662 m (SD 156) in September. The dive depth decreased during October and November when the whales were transiting to their wintering ground (mean = 571 m, SD 197, Table 1 and Fig. 5). In January, when sea ice would have forced the whales further offshore, average dive depth increased to 1064 m (SD 323) and the maximum depth of dives increased to ~1600 m. There was no apparent difference in the mean daily maximum dive between males (690 m), females (699 m) or the one female with a calf (702 m). A covariate model including year, day of the year and gender did not explain more than 22% of the variability in the depth of the daily maximum dives (ANCOVA). However, day of the year alone influenced the maximum depth of dives with the days inside Scoresby Sound (day of the year <300) having significantly shallower maximum depths than the days outside Scoresby Sound (>300). When the narwhals conducted deep

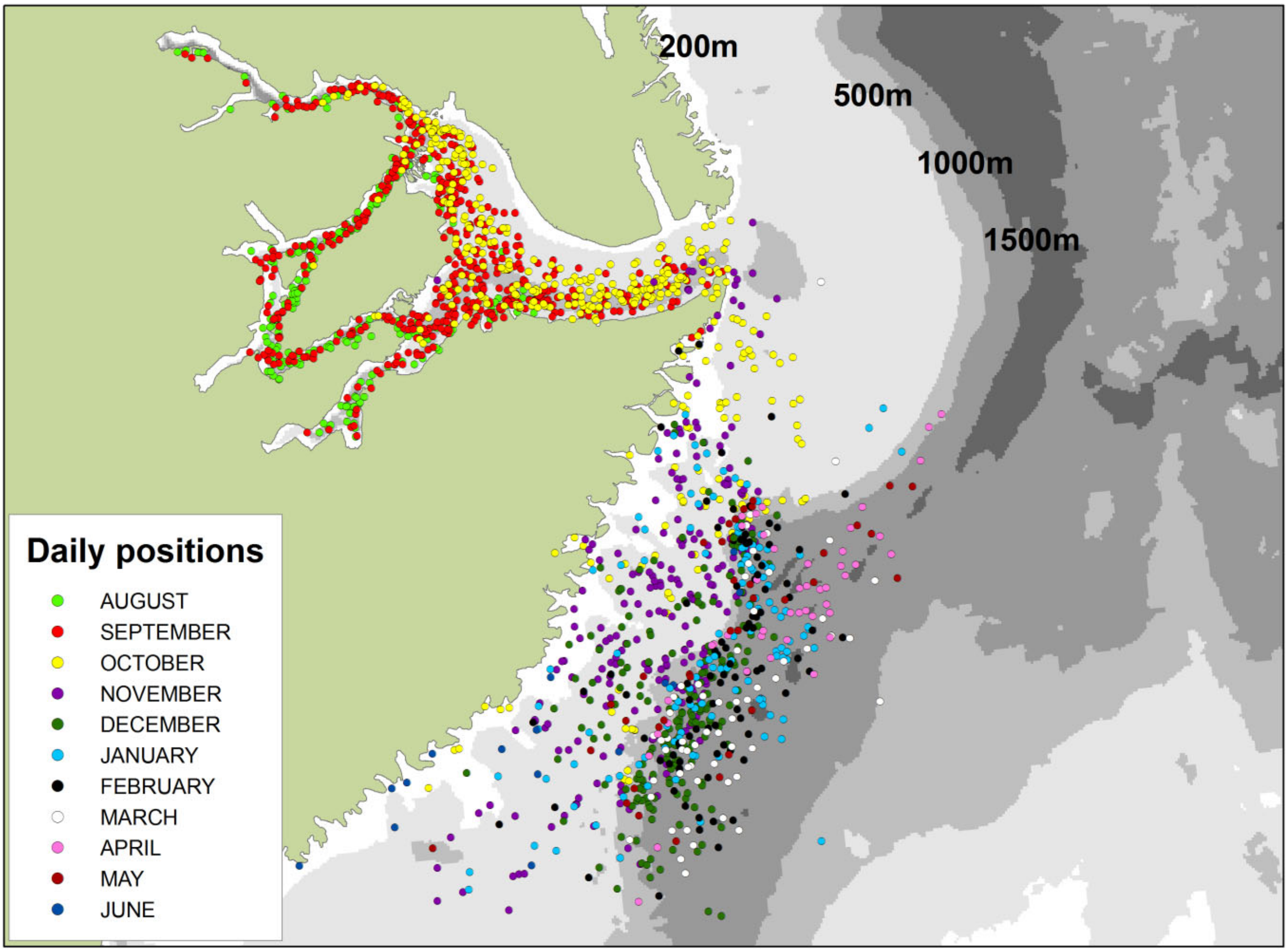

Figure 3 Average positions calculated for each day with good-quality transmissions, distributed by month for all 28 narwhals tagged in 2010–2013.

dives (>600 m) in the offshore area delineated by 50% of the kernel area usage, the daily maximum dives on average covered 58% (SD 20) of the actual distance to the seabed, suggesting that the narwhals were targeting mesopelagic prey. Nevertheless, some dives also reached the seabed where benthic prey items could be found (Fig. 6).

It was difficult to find suitable bottom for trawling in shallow waters in Scoresby Sound and the soft bottom in the northern part of the sound also hampered trawling. Nevertheless, Greenland halibut was caught in all 10 hauls (depth range: 381–590 m) and average density was 116 kg km^{-2} (SE 32, Fig. 4) with length ranging from 10 to 69 cm. The bottom temperature was low, ranging from 0.8 to 1.1°C. In total, 19 fish species were recorded (see Supporting Information Table S1), but aside from Greenland halibut, only polar cod was detected in significant numbers with a density of 87 kg km^{-2} (SE 11). The polar cod were, however, small (7–26 cm).

The bottom was rough in the offshore area outside Scoresby Sound. The shallow waters along the coast and in the north-eastern part of the survey area were particularly difficult to sample with the trawl. A total of 44 hauls (depth range: 118–1459 m) indicated low bottom temperatures (range: −1.2 to 1.8°C, with negative temperatures at 16 of the 44 stations). In total, 44 fish species were recorded and Greenland halibut was caught in 18 of the 44 hauls (Supporting Information Table S2). Catches were low, with an average density of 99 kg km^{-2} (SE 52) and lengths ranging from 18 to 93 cm. Again, polar cod was, aside from Greenland halibut, the only other significant contributor with a density of 19 kg km^{-2} (SE 7).

Discussion

The presence and movements of narwhals in Scoresby Sound is largely influenced by the seasonal formation and decay of sea ice. No modern description of the annual cycle of sea ice formation exists from Scoresby Sound, but the general pattern is that fast ice forms in the inner parts of the fjord from mid-September, and by late November, only the outer part of the fjord is ice free (Koch, 1945). Because of current and wind conditions the opening of Scoresby Sound is usually free of ice during winter. The sea ice starts to break up in late June, but

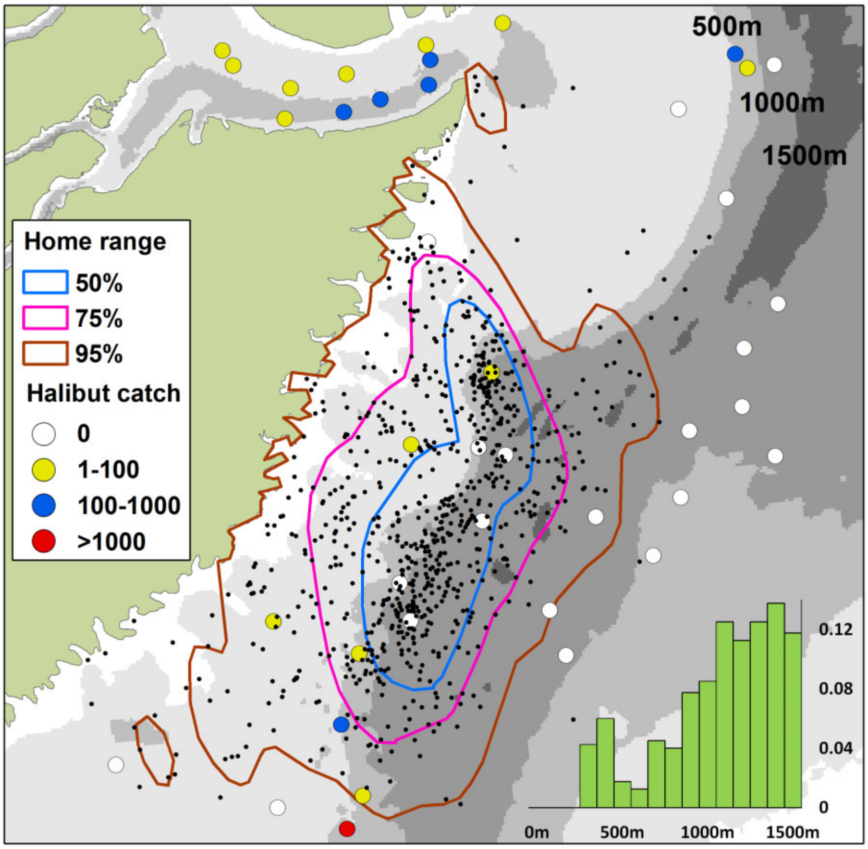

Figure 4 Winter area usage by narwhals from Scoresby Sound. Positions of whales are indicated by black dots (daily averages from positions of LC = 1–3), kernel home ranges are shown with the blue line (50%: 7068 km^2), pink line (75%: 15 374 km^2) and brown line (95%: 34 581 km^2). Bathymetry is shown in shades of grey for 200, 500, 1000 and 1500 m and catches of Greenland halibut during a scientific fishery in 2006 are shown as open circles (no catches), yellow (1–100 kg km^{-2}), blue (100–1000 kg km^{-2}) and red (>1000 kg km^{-2}) circles. The histogram inserted to the right shows relative frequency of water depths at the narwhal positions within the 50% kernel home range area.

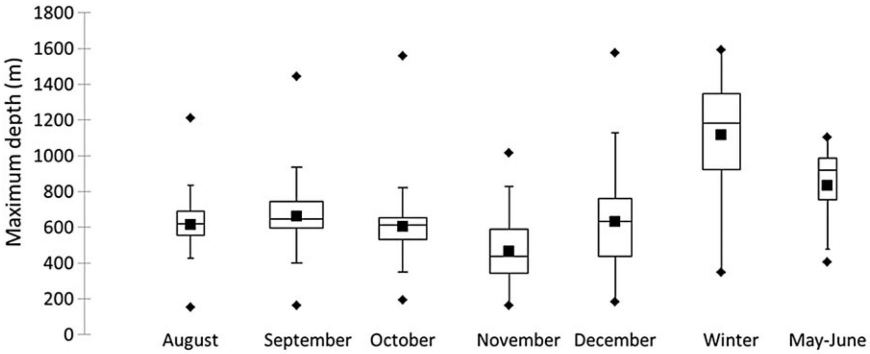

Figure 5 Box plot of the seasonal changes in daily maximum depth of dives from 28 narwhals tagged in Scoresby Sound in 2010–2013. Note that the maximum depth was only available every other day. Mean values are represented by a filled square, and the black line inside the empty box is the median. The limits of the empty boxes represent the first and third quartiles and the black diamonds show the range of values. Winter includes data from January through April. Significant differences were detected between winter and all other months, between May–June and all other months, and between November and all other months (ANOVA, Tukey post-hoc analysis).

the fjord and tributaries are not ice free until mid- or late-July. Therefore, narwhals cannot enter the inner parts of the fjord until mid-July and they have to abandon them again during November to avoid ice entrapment when fast ice is being formed.

In East Greenland, narwhals are found as far south as 64°N but there are no sightings at the southern tip of Greenland (60°N) or along the northern coast of East Greenland (Dietz *et al.*, 1994). In West Greenland, narwhals are not found further south than 66°N and it is therefore unlikely that there has been any significant genetic exchange between narwhals in East and West Greenland since the last glaciation, that is, >10 000 years ago. Despite the long separation and the different habitats in the two areas, there are still some striking behavioural similarities between the two populations. Both populations have strong affinity for summering grounds in coastal areas usually in front of glaciers or in areas where glaciers have receded (Dietz *et al.*, 2008; Heide-Jørgensen

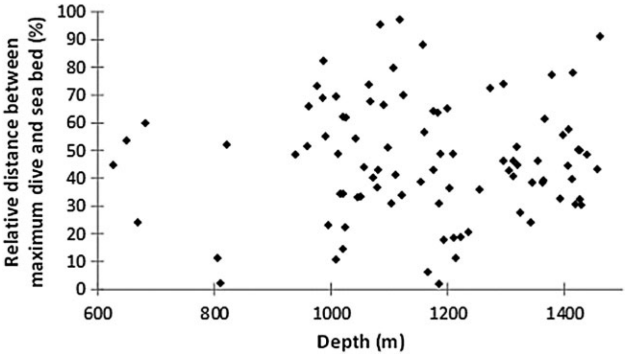

Figure 6 Relative distance from the depth of the daily maximum to the seabed at the position of the dives during winter for the 50% kernel area (Fig. 4). Only dives deeper than 600 m and dives with a positive distance to the seabed are shown. The average daily maximum diving depth reached on average 42% (SD 20) of the distance to the seabed.

et al., 2012*a*). A comparison of the following four behavioural traits between narwhals from Scoresby Sound and five narwhal populations in Baffin Bay and Hudson Bay is useful for assessing the behavioural predictability between isolated narwhal populations.

The predictable fall migration

The summering grounds in the inner parts of Scoresby Sound around Milne Land and tributaries were almost completely abandoned in October when the whales headed out of the fjord, and some were already at their wintering ground. Aerial surveys conducted in September have showed that narwhals were primarily located in Hall Bredning and the opening of Scoresby Sound (Larsen *et al*., 1994). Our data showed that the main exodus from Scoresby Sound occurred in October at least a month prior to ice formation inside the fjord. Intensive travelling activity was also evident in at least five narwhal populations in Baffin Bay and Hudson Bay who also left their summering grounds in October and spent November travelling towards their wintering grounds (Dietz & Heide-Jørgensen, 1995; Dietz *et al*., 2001, 2008; Heide-Jørgensen *et al*., 2002, 2003; Westdal, Richard & Orr, 2010). The timing of the exodus from summering grounds is similar for all these populations and does not seem to be triggered by fast ice formation, which for all localities occurs about a month later. Other factors like day length may initiate the migration to offshore areas.

One feature that distinguishes East Greenland narwhals from those in Baffin Bay is the short travelling distances during migrations. Ten narwhals tagged in Eclipse Sound travelled on average twice as many kilometres per day (56 km day^{-1}, SD 9.7) as those from Scoresby Sound and there was no significant difference between males and females (cf. Heide-Jørgensen *et al*., 2002). Similarly, narwhals of both sexes from Melville Bay travelled much farther than those from Scoresby Sound (40 km day^{-1}, Dietz & Heide-Jørgensen, 1995). However, the travel distances of the whales were close to identical to measurements from Baffin Bay evaluated both at 0.5–5 h (mean 4.2 km h^{-1}, SD 1.7) and 5–15 h (2.7 km h^{-1}, SD 1.0) intervals between consecutive positions (Dietz & Heide-Jørgensen, 1995), indicating a more convoluted movement pattern of the East Greenland whales.

The predictable wintering habitat

None of the whales spent time in the polynya in the outer part of Scoresby Sound where open water or at least highly moveable pack ice is available throughout the winter (Koch, 1945). Instead, the narwhals moved south and made visits to fjords along the Blosseville Coast. The wintering grounds, where the whales spent 6–8 months, were located along the shelf contour where water depth increases from 500 to 1500 m over a distance of <20 km. The whales generally remained offshore in the latitude range 68–69°N and mainly made north-south movements along the 1000 m depth contour perhaps in response to the south-going current and ice drift. Narwhals in Baffin Bay-Hudson Bay also visit coastal areas during the fall migration and are attracted to deep-water areas at the edge of the continental slope during winter (op. cit.). Comparison of the 50% kernel area usage during winter showed that the size of the wintering ground for narwhals in East Greenland (7000 km^2) was within the range of the wintering areas used by four populations of narwhals in Baffin Bay (2000–22 000 km^2, Fig. 7). Similarly, the 95% kernel area usage estimate was 35 000 km^2 for the East Greenland narwhals compared with estimates ranging from 7000 km^2 to 133 000 km^2 for populations in Baffin Bay and Davis Strait (Dietz *et al*., 2008; Westdal *et al*., 2010).

The site fidelity

The one whale recaptured with its transmitter at the tagging site a year after instrumentation clearly supports the extreme site fidelity of narwhals to their summering grounds. The two whales tracked for >10 months were not far from the entrance to Scoresby Sound when their tags failed, but did not actually reach the site where they were tagged the previous year. Hunting of narwhals near Scoresby Sound started in May in both years (2011 and 2014), thus other whales must have arrived at the hunting areas earlier than June. None of the whales showed any affinity to the other East Greenland hunting areas, that is, from Kangerlussuaq (68°28’N 32°19’W) and south to Sermilik (Tasiilaq area, 66°N 38°W). Although their summer destinations were not determined, the three aforementioned whales support the idea that narwhals migrate back to the Scoresby Sound fjords, and do not support the hypothesis that Scoresby Sound narwhals summer in fjords south of Kangerlussuaq, as suggested by Nielsen & Meilby (2013). The most likely scenario is therefore that these other localities in East Greenland are supplied by whales that summer in those same fjords and that whales in these areas are not connected to whales from Scoresby Sound. Following this, the hunt for narwhals in the Scoresby Sound and the Kangerlussuaq-Sermilik areas must be managed separately.

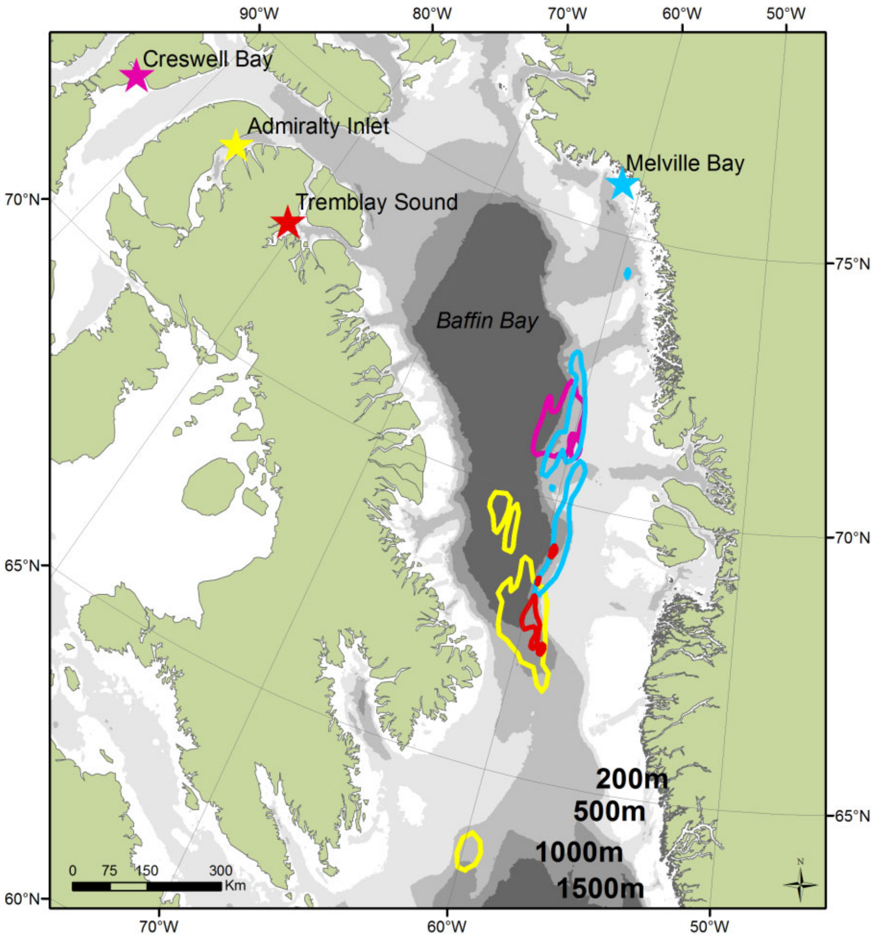

Figure 7 Winter area usage by narwhals in Baffin Bay. Winter kernel home ranges (50%) of daily average positions of good quality (see Supporting Information) are shown with blue line for whales from Melville Bay (15 000 km^2), pink line for whales from Creswell Bay (9000 km^2), yellow line for whales from Admiralty Inlet (22 000 km^2) and red line for whales from Tremblay Sound (2000 km^2). Bathymetry is shown in shades of grey for 200, 500, 1000 and 1500 m. Data from Heide-Jørgensen *et al.* (2012*a*).

The narwhal populations in East Greenland and the Greenland Sea likely constitute a metapopulation with limited exchange between summering stocks, as also seen in Baffin Bay (Heide-Jørgensen *et al*., 2012*a*).

The predictable feeding grounds

In Baffin Bay, narwhals are known to feed intensively on Greenland halibut during winter and to display extensive diving activity targeting areas and depths with Greenland halibut (Laidre *et al*., 2003, 2004). During summer, narwhals feed less intensively and often have empty stomachs (Laidre & Heide-Jørgensen, 2005). Samples of narwhal stomachs collected from the hunters in Scoresby Sound have similarly indicated low feeding activity during summer with few food remains from squid, polar cod and shrimp (Heide-Jørgensen *et al*., 2014). No remains of Greenland halibut were detected but Greenland halibut were widely distributed over the narwhal habitat both in the outer part of Scoresby Sound and offshore on the wintering ground, and the whales generally maintained diving activity to depths where Greenland halibut can be found. The catchability in the trawl survey of the different fish species is unknown and probably varies between species but it is assumed that all demersal fish in the trawled area were caught. The trawl is about 6 m high, which means that abundance of bathypelagic and pelagic species such as polar cod is underestimated. Further, Greenland halibut is known to make feeding migrations into the water column, which also would lead to an underestimate of the abundance (Vollen & Albert, 2008).

The fishery for Greenland halibut along and on the East Greenland shelf has been increasing steadily since 1991 and reached 10 000 tons in 2009 (Boje & Sünksen, 2010). The fishery is mainly restricted to the area with depths between 500 m and 1000 m, from 61°N 41°W in the southwest to 68°N 40°W, with a major increase in catches north of 67°30’N. At present, the fishery mainly affects narwhals wintering further south, but if it increases in the northern area, it may also affect the population from Scoresby Sound. Although potential conflicts with Greenland halibut fisheries are similar in East and West Greenland, both Greenland halibut and polar cod densities were <10% of what could be expected at similar water depths in narwhal habitats in Baffin Bay (Laidre *et al*., 2004).

Another unknown factor is the presence of capelin (*Mallotus villosus*), a species whose importance may increase with ocean warming (Rose, 2005). Capelin is occasionally seen in Scoresby Sound (Heide-Jørgensen unpubl. data) and analyses of stable isotopes in narwhal skin samples collected during August in Scoresby Sound suggest that capelin may be an important prey item (Watt, Heide-Jørgensen & Fergusen, 2013). The 'Icelandic capelin stock' has shifted its distribution to areas north of Iceland and towards East Greenland in recent years, probably driven by increasing sea temperatures. Capelin is now abundant and widely distributed along the east coast of Greenland and on the shelf areas where narwhals occur in winter (Vilhjálmsson, 2006, 2007; ICES, 2014). The observed bottom temperatures in offshore areas are consistent with the thermal tolerance of capelin (Rose, 2005) and it is likely that capelin constitute an increasingly important part of the narwhal's diet during winter. Even though the narwhals made their deepest dives during winter, they still on average only made dives halfway to the seabed, which suggests mesopelagic feeding, in agreement with feeding on capelin, squid and Greenland halibut. Although the relative depth of dives (relative to the seabed) has not been determined for other narwhal populations, it seems like the mesopelagic feeding shown by East Greenland narwhals may be the most important ecological difference between narwhals in East Greenland and those in other areas (cf. Watt *et al.*, 2015).

Narwhals from Scoresby Sound travelled a distance of ~350 km between summering and wintering habitats. This is the shortest migratory route of all known narwhal populations. Narwhals in Melville Bay travel ~800 km to their wintering ground, whereas populations in Hudson Bay and Admiralty Inlet, Canada, travel ~1500 km (Dietz & Heide-Jørgensen, 1995; Dietz *et al.*, 2008; Westdal *et al.*, 2010). Populations in Somerset Island hold the record of traveling ~1700 km between summer and wintering grounds (Heide-Jørgensen *et al.*, 2012*a*). The short distance between summering and wintering grounds in East Greenland may compensate for the low density of halibut on the wintering ground, compared with areas west of Greenland.

This study demonstrates how behavioural traits in a marine population have been maintained despite >10 000 years of separation. Although East Greenland narwhals have been shown to be genetically distinct from narwhals in West Greenland, there is still a remarkable behavioural consistency, not just in behavioural traits and movements in relation to sea ice formation, but also in diving behaviour, feeding ecology and habitat selection. The predictability in culturally inherited migration patterns and in habitat selection among narwhal populations is certainly different from the two other Arctic cetaceans, the bowhead whale (*Balaena mysticetus*; cf. Nielsen *et al.*, 2015; Lydersen *et al.*, 2012) and belugas (*Delphinapterus leucas*; cf. Suydam *et al.*, 2001). Site fidelity and lack of behavioural plasticity renders narwhal populations vulnerable to changes in their habitats, especially the rapid reduction in pack ice on their wintertime feeding habitat, which has been observed over the past two decades, combined with increased traffic and industrial activities in new ice-free areas (Laidre *et al.*, 2008; Williams, Noren & Glenn, 2011; Heide-Jørgensen *et al.*, 2012b; Reeves *et al.*, 2014).

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. All Argos positions obtained from the 28 narwhals.

Table S1. List of species or groups of species recorded in Scoresby Sound with observed maximum weight (kg), maximum number, minimum and maximum depth (m) and minimum, maximum bottom temperature °C and most northern position, respectively.

Table S2. List of species or groups of species recorded off North East Greenland in 2006 with observed maximum weight (kg), maximum number, minimum and maximum depth (m) and minimum, maximum bottom temperature (°C) and most northern position, respectively.