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Oceanic movements, site fidelity and deep diving in harbour porpoises from Greenland show limited similarities to animals from the North Sea

Nynne H. Nielsen[1,2,*], Jonas Teilmann[2], Signe Sveegaard[2], Rikke G. Hansen[1], Mikkel-Holger S. Sinding[1], Rune Dietz[2], Mads Peter Heide-Jørgensen[1]

[1]Greenland Institute of Natural Resources, 3900 Nuuk, Greenland
[2]Aarhus University, Department of Bioscience, 4000 Roskilde, Denmark

ABSTRACT: Harbour porpoises *Phocoena phocoena* are common in continental shelf areas of the North Atlantic, but little information is available on their occurrence outside coastal areas. In this study, 30 harbour porpoises were actively caught in West Greenland and instrumented with satellite transmitters to document their seasonal movements and diving behaviour. The porpoises displayed long-range oceanic movements within the North Atlantic, especially during winter/spring where they moved over areas with water depths >2500 m. While offshore, 2 females demonstrated an average maximum dive depth of 248 m, with the deepest dive reaching 410 m. This behaviour is in contrast to 71 porpoises tagged in Danish waters of the North Sea which did not leave the continental shelf but showed a preference for areas with shallow waters year round, even when at the edge of the continental shelf where greater depths were available. Six tags from Greenland transmitted long enough (up to 3 yr) to demonstrate extensive movements and strong site fidelity to the tagging site in West Greenland the following summer. This study documents that harbour porpoises use oceanic habitats and can dive to depths that enable mesopelagic foraging, while repeatedly demonstrating summer site fidelity to coastal areas.

KEY WORDS: Argos satellite tracking · Oceanic movements · North Atlantic · Danish waters · Diving behaviour · Mesopelagic prey · Habitat selection

INTRODUCTION

Harbour porpoises *Phocoena phocoena* are thought to be closely associated with continental shelf areas (depth <200 m) (Read & Westgate 1997), where most surveys of harbour porpoise abundance have been conducted (Forney & Barlow 1998, Hammond et al. 2013, Hansen & Heide-Jørgensen 2013). Little information is available on their distribution outside coastal areas despite their potential for moving over large areas (Johnston et al. 2005). Compared to other toothed whales, harbour porpoises are referred to as living 'life in the fast lane' due to their early maturity, high pregnancy rate and short lifespan (Read & Hohn 1995), and moreover, harbour porpoises have a high energy demand. Their small size gives them a large surface to body volume ratio (see Kleiber 1947), which induces higher energy loss through radiation and thermal conduction compared to larger cetaceans. Despite large seasonal variations in the blubber layer that serves as an adaptive mechanism to cope with water temperatures from subarctic to temperate habitats (Lockyer et al. 2003a), living in these habitats requires porpoises to locate high densities and predictability of prey to maintain basal metabolism and blubber insulation (Koopman 1998, Wisniewska et al. 2016). To keep up with the energy demand, they exploit a wide range of prey species, mainly fish, but also cephalopods and copepods, and thus porpoises are

*Corresponding author: nel@ghsdk.dk

often referred to as opportunistic feeders. However, in some cases their choice of prey may be dependent on its caloric content (Fontaine et al. 1994, Lockyer et al. 2003b, Heide-Jørgensen et al. 2011, Spitz et al. 2012, Leopold et al. 2015, Andreasen et al. 2017; for a review, see Santos & Pierce 2003).

Harbour porpoises are believed to avoid sea ice and sub-zero temperatures, and they seem to prefer certain sea surface temperatures (SSTs) (Wingfield et al. 2017). Other environmental variables such as distance to coast, bottom salinity and bathymetry also affect the distribution of harbour porpoises (Edrén et al. 2010, Gilles et al. 2011).

Mitochondrial DNA studies have suggested that the Northwest and Northeast Atlantic populations are somewhat discrete, and that exchange of genes across the Atlantic rarely occurs (Rosel et al. 1999; see Andersen 2003 for a review). Porpoises from West Greenland are believed to be genetically separate from other populations in both the Northeast (Norway, North Sea and Ireland; Andersen et al. 2001) and the Northwest and Central Atlantic (Gulf of Maine, Gulf of St. Lawrence, Newfoundland and Iceland, Tolley et al. 2001). However, porpoises from West Greenland are thought to be most closely related to porpoises from the Gulf of St. Lawrence (Rosel et al. 1999).

Information on the ecology of West Greenland harbour porpoises includes studies on the abundance, distribution and life history of animals on the continental shelves (Teilmann & Dietz 1998, Lockyer et al. 2001, 2003b, Heide-Jørgensen et al. 2011, Hansen & Heide-Jørgensen 2013). Porpoises from West Greenland use the productive waters of the West Greenland shelf to prey on a variety of species, with capelin *Mallotus villosus*, Arctic cod *Boreogadus saida* and cephalopods being the main prey (Heide-Jørgensen et al. 2011). Harbour porpoises are subject to hunting by humans year round in Greenland, although most of the hunt takes place in August–October, suggesting that these months also reflect the main occurrence of harbour porpoises on the coastal shelves (NAMMCO 2013). The highest densities of porpoises in Greenland are located on the southwest coast (Teilmann & Dietz 1998), and this is also where most of the hunting of porpoises takes place.

To gain insight into the ecology and population discreteness of harbour porpoises in West Greenland, 30 harbour porpoises were instrumented with Argos satellite transmitters between 2012 and 2014. The transmitters provided information on the porpoise movements and habitat preferences; these data were compared to those of 71 harbour porpoises from the North Sea population tagged in Danish waters between 1997 and 2015.

MATERIALS AND METHODS

Capture and handling of harbour porpoises

Thirty harbour porpoises were actively live-captured on the continental shelf ca. 50 km south-west of Maniitsoq, West Greenland, in July 2012 (n = 2); July, September and October 2013 (n = 6, 3 and 5, respectively); and July 2014 (n = 14). Two 6.30 m fibreglass dinghies with 150 hp outboard engines were used to spot and catch the porpoises. The boats were operated by 2 experienced local hunters. One boat (net launch boat, with one person) carried a monofilament surface gill net, 5 m deep and 50 m long with stretched mesh size of 20 cm. The nets were fitted with an upper float line and a bottom lead line to keep the nets vertically oriented at the surface of the water. When a porpoise was spotted, the gill net was quickly launched and the porpoise was herded by the second boat (herd boat, with 3 persons). The boats kept a close lookout for the porpoise while the herd boat followed it and kept it on the starboard side until herded into the net. Porpoises avoided the boats and thus reacted to being herded in a specific direction. As soon as entanglement of the porpoise was observed by movements at the float line or the animal being visible at the surface, both boats quickly went to the net, where the engines were stopped to prevent further stress of the animal. The animal was then removed from the net and lifted into the boat on a foam pad where it was dosed regularly with sea water. This was done to prevent the skin from drying and to keep the animal breathing regularly. The duration of the herding was on average 15–20 min. On a few occasions, 2 porpoises were caught at the same time and one boat kept the second porpoise at the surface in the net until the other boat had finished instrumenting the first animal. Information on sex, mass and length was collected before release (Table 1). The handling time was on average 5 min, and all porpoises quickly swam away with regular surfacings upon release.

The 71 porpoises tagged in Danish waters were caught incidentally in pound nets. The fisherman would then contact the research team that reached the net within 24 h. Information on the 71 harbour porpoises caught in Danish waters is provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/m597p259_supp.pdf.

Table 1. Basic information on 30 harbour porpoises instrumented with satellite transmitters in West Greenland 2012–2014. Superscript numbers indicate porpoises caught together (presumed mother/calf pairs). The exact daily maximum dive depth was recorded for PTT ID 7617 and 7618. The remaining dive depths were calculated from the binned dive depths of the Mk10 tags. PTT ID: platform transmitter terminal identification; NA: data not available

PTT ID	Type	Deployment	Tag longevity (d)	Sex	Length (cm)	Body mass (kg)	Initial shelf duration (d) prior to offshore movement	Maximum dive depth (m)		Median maximum dive depth (m)		Days with dive data
								Shelf	Offshore	Shelf	Offshore	
7617[a,b]	SPLASH	25 Jul 12[1]	476	F	128	NA	2	168	390	168	240	104
7618[a,b]	SPLASH	25 Jul 12[1]	422	F	156	NA	7	410	410	265	261	150
20160[a]	SPOT 5	7 Jul 13	243	M	140	43	170	–	–	–	–	–
20164[a,b]	SPOT 5	7 Jul 13	376[d]	F	128	41	163	–	–	–	–	–
20165[a]	SPOT 5	10 Jul 13	393	F	115	28	204	–	–	–	–	–
20166[a]	SPOT 5	7 Jul 13	227	M	136	39	139	–	–	–	–	–
20167[a]	SPOT 5	10 Jul 13	146	F	124	31	2	–	–	–	–	–
20169[a]	SPOT 5	6 Jul 13	268	M	120	31	218	–	–	–	–	–
21791[a,b]	SPOT 5	16 Jul 14	649	F	111	NA	179	–	–	–	–	–
21792[a,b]	SPOT 5	30 Jul 14	1047	M	130	NA	71	–	–	–	–	–
21793	SPOT 5	17 Jul 14	95	F	123	NA	–	–	–	–	–	–
22849	MK10[c]	25 Sep 13[2]	19	F	NA	30	–	150	–	100	–	5
22850	MK10	3 Oct 13	71	F	140	43	15	250	250	200	150	10
22853[a]	MK10[c]	25 Sep 13[2]	29	F	166	NA	7	300	250	200	150	3
22854	MK10	22 Jul 14	138	M	130	NA	–	350	–	200	–	111
27261	MK10[c]	2 Oct 13[3]	64	M	125	33	–	250	–	150	–	16
27262	MK10[c]	2 Oct 13[3]	16[d,e]	F	150	NA	–	300	–	275	–	4
37227[a]	MK10[c]	2 Oct 13[4]	46	F	129	47	4	100	150	100	75	3
37228	MK10[c]	2 Oct 13[4]	66	F	150	53	–	200	–	150	–	15
37235	MK10[c]	27 Sep 13	67	F	126	35	–	250	–	150	–	8
93096	MK10	16 Jul 14	130	M	120	NA	–	400	–	200	–	109
93100	MK10	22 Jul 14	170[d]	M	145	NA	–	400	–	250	–	20
93102	MK10	16 Jul 14	148	M	149	NA	–	400	–	200	–	121
228491	MK10	22 Jul 14	146	F	123	NA	–	350	–	200	–	99
228501	MK10	17 Jul 14	137	F	125	NA	–	350	–	200	–	119
272611	MK10	16 Jul 14	130	M	152	NA	–	350	–	200	–	118
272621	MK10	22 Jul 14	134[d]	M	140	NA	–	400	–	200	–	104
372271[a]	SPOT 5	11 Jul 14	478	M	127	39	193	–	–	–	–	–
372281[a,b]	SPOT 5	18 Jul 14	1043	M	120	NA	216	–	–	–	–	–
372351	MK10	16 Jul 14	136	F	135	NA	–	350	–	200	–	118

[a]Animals that moved offshore (<200 m for 20 out of 30 d)
[b]Animals that returned to the tagging area
[c]Transmitters with a battery defect
[d]Porpoises shot by a hunter
[e]Tags that ended their transmission due to the porpoise being shot

Instrumentation with satellite transmitters

The animals in West Greenland were instrumented with 3 types of Argos satellite-linked transmitters (2 SPLASH: 80L × 19W × 49H mm, 76 g; 18 Mk10: 108 × 41 × 21 mm; 75 g; and 10 SPOT5 tags: 81 × 19 × 51 mm; 49 g), from Wildlife Computers, modified for fin-mounted use on harbour porpoises. The tags were attached to the dorsal fin using 3 delrin pins (5 mm diameter) covered by silicone tubing, increasing the total diameter of the pins to 6 mm. These pins were attached to the tag by stainless steel nuts and pushed through holes drilled in the fin with a sterilized 7 mm cork borer mounted on a battery drill. The extra millimetre facilitated room for tissue swelling and reduced the risk of pressure necrosis around the pins. The pins were secured on the opposite side of the fin to a backing plate (2 mm rubber conveyer belt) with stainless steel nuts, and the distal part of the pins was flattened to secure the nuts. In order to collect data for as long as possible, the tags were not designed to release from the animal, as used for other porpoises instrumented with fin-mounted satellite transmitters (Teilmann et al. 2007). Both the tag and backing plate were lined with closed-cell neoprene to prevent abrasion. For details on the tagging procedure of the Danish porpoises, see Teilmann et al. (2007) and Sveegaard et al. (2011).

Data analysis

The instrumented SPOT5 tags were designed to provide only the location of the porpoise, while the SPLASH and Mk10 tags provided information on location, time and pressure (depth). These were sampled at a default rate of every second, and stored in 6 h summary histograms that were relayed to the satellite during the following 24 h. The histograms were sampled in four 6 h bins: 01:00–07:00, 07:00–13:00, 13:00–19:00 and 19:00–01:00 h. For SPLASH tags, the user-defined intervals were 0 m, then 5 m bins up to 30 m, then 10 m bins up to 90 m and then >90 m. For Mk10 tags deployed in 2013, the intervals were 5, 10, 25 and 50 m, then 50 m bins up to 500 m and then >500 m. For Mk10 tags deployed in 2014, the intervals were 1, 2, 10, 25 and 50 m, then 50 m bins up to 450 m and then >450 m. In addition, the SPLASH tags also provided information on the maximum dive depth (m) during the past 24 h. All tags sampled and transmitted histograms of maximum depth for each dive in 14 user-defined intervals. In order for the battery to hold the charge as long as possible, the tags were programmed to wake up and record data every fourth day (SPOT5 PTT IDs: 21791, 21792, 21793, 372271, 372281) and every second day for all remaining tags.

The tags were limited with regard to data collection, and the 14 pre-defined bin intervals were based on the assumed dive range of the porpoises. As no one had tagged harbour porpoises in West Greenland prior to this study, the first tags (2012) were programmed following previous tag deployments on porpoises in Danish waters (Teilmann et al. 2007). For the second deployment (2013) it was clear that porpoises in West Greenland were diving to greater depths and thus the bin intervals were changed to cover their diving range. For the last deployment (2014) the bin intervals were altered to collect data on porpoise surface time for abundance estimations in West Greenland (Hansen et al. in press). In order to register the capacity for deep dives, the last bin intervals (>90, >500 and >450 m, respectively) registered all potential dives exceeding this depth.

The first Mk10 tags deployed in 2013 (n = 8, Table 1) were acknowledged by the manufacturers to be subjected to a defect, which resulted in sudden discharging of the batteries leading to low tag lifespan. The mean lifespan of these 8 tags was 47 d (range: 16–71 d, SD = 23) and significantly shorter than the other Mk10 tags (n = 10) that transmitted for a mean of 141 d (range: 130–170 d, SD = 12, 2-sample *t*-test, t_{16}, $p < 0.0001$).

The Argos positions of the porpoises from West Greenland were obtained from the Argos satellite data processing system, filtered using the R (version 3.3.3, R Development Core Team 2008) package 'argosfilter' (Freitas et al. 2008), while the comparable SAS-routine (SAS 9.3), Argos-Filter v7.03 (Douglas 2006) was used for porpoises tagged in Danish waters. The accuracy of locations was assessed by Argos location codes (LC) B, A and 0–3, and an average position was calculated for all good-quality positions (LC = 1–3) for each transmission day. If no good-quality positions were available, low-quality positions (LC = 0, A and B) were used for the subsequent analysis. The ranging areas for the 2 porpoise populations were estimated by creating minimum convex polygons (MCPs) using the freeware QGIS (version 2.18, QGIS Development Team 2017). To visually display the density of harbour porpoises in West Greenland and the North Sea, the 'Heatmap' plugin in QGIS 2.18 was used and 50% and 95% kernel densities were added. 'Heatmap' uses kernel density estimation to create a density raster from the porpoise positions, calculated based on the number of positions within a grid cell. The density was weighted by individual PTT ID. The radius (band-width) was based on inspection of kernel contours during tests of alternate band-width as recommended by Kie (2013). Upon testing, the radius were set to 90 000 for porpoises tagged in West Greenland and 50 000 for porpoises tagged in Denmark, and the cell size was set to 50 km^2 and 4 km^2, respectively.

The bathymetry (Jakobsson et al. 2012) at each porpoise position was calculated in ArcGIS. For the porpoises tagged in Greenland, we used map projection UTM Zone 25N, WGS84, and for the porpoises tagged in Denmark, we used map projection UTM Zone 32N, WGS84. XLSTAT version 2014.6.01 was used for statistical analysis. To analyse porpoise movement in relation to sea ice, the monthly sea ice distribution in 2013, 2014, 2015 and 2016 was obtained from sea ice charts of the Labrador Sea and off the coast of Newfoundland (Danish Meteorological Institute 2017) and plotted in QGIS 2.18. The charts measured the sea ice concentrations in tenths in the following categories; <1/10 = open water, 1/10–3/10 = very open drift ice, 4/10–6/10 = open drift ice, 7/10–8/10 = close drift ice, 9/10 = very close drift ice, 10/10 = fast ice. Only sea ice concentrations >1/10 were included in the analysis. Sea surface temperatures (SST) were downloaded from Copernicus ((http://marine.copernicus.eu/services-portfolio/access-to-products/) and analysed in QGIS 2.18.

The monthly maximum sea ice distribution for West Greenland was visually inspected for the years 2013–2016, to cover the movement of the instrumented porpoises, and the maximum ice distribution was located and compared with the distribution of the instrumented harbour porpoises in the same month. Similarly, North Atlantic SSTs were obtained and added to the maps for inter-annual comparison.

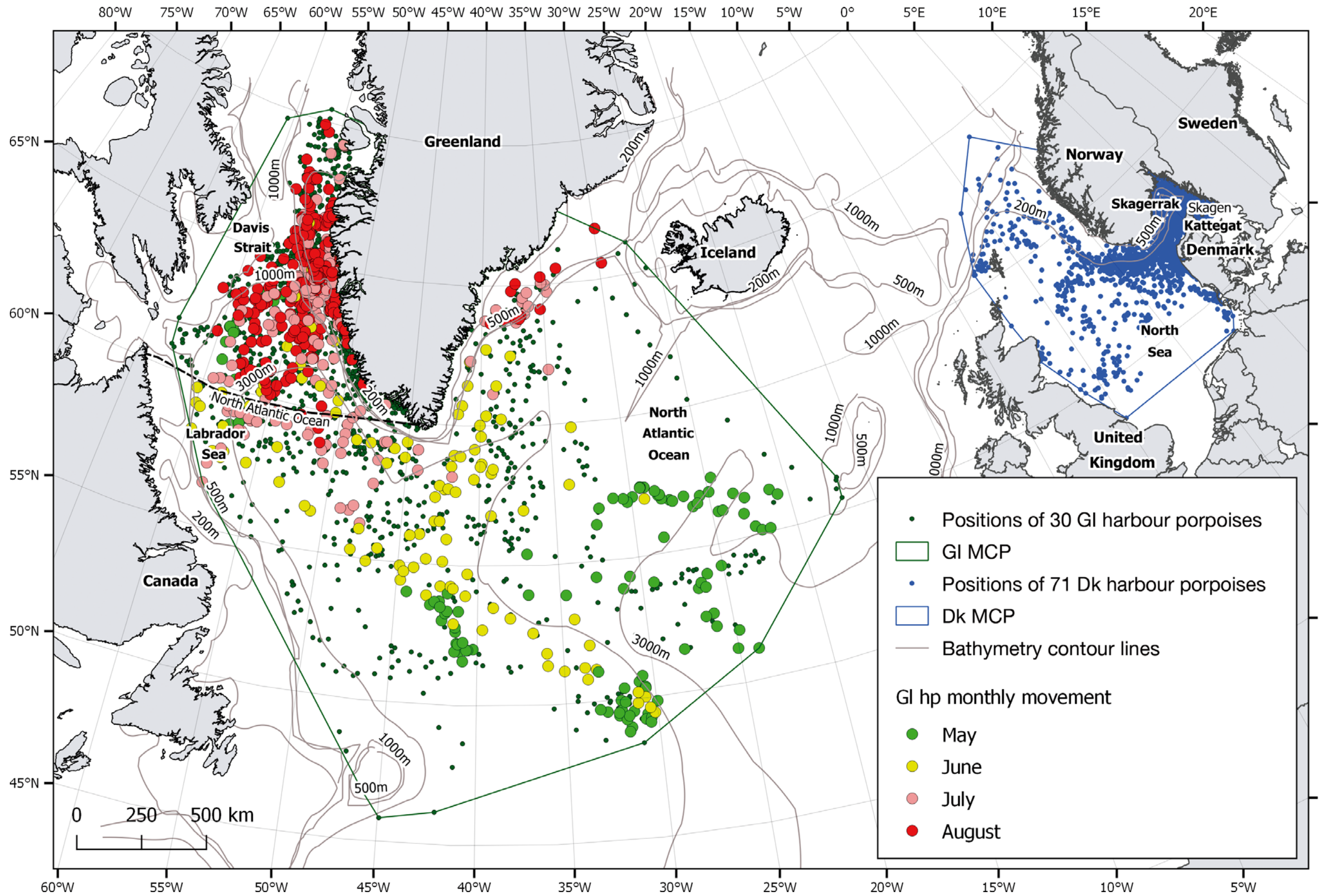

Fig. 1. Minimum convex polygons (MCP) of the total area covered by 30 harbour porpoises tagged in West Greenland (Gl, green line), and 71 porpoises tagged in Denmark (Dk, blue line). Small dots represent all recorded satellite positions of porpoises tagged in West Greenland (green) and Denmark (blue) for the duration of the tags. Larger dots highlight the positions of porpoises tagged in West Greenland in May (green), June (yellow), July (pink) and August (red), thus illustrating the return of porpoises to the East or West Greenland shelf over this period. The dashed line indicates the limit of the North Atlantic Ocean defined in this study

Of the 71 porpoises tagged in Denmark, 30 were tagged off Skagen in the Skagerrak (Fig. 1, Table S1). These individuals are believed to belong to a large population residing in the North Sea and adjacent waters. The remaining 41 porpoises were tagged in the Kattegat or the Danish Belt Seas; however, only locations north of the Kattegat were included in the data comparison (Sveegaard et al. 2015). The depths in the Kattegat and the Belt Seas are generally <50 m and were considered less comparable to the depths in West Greenland.

All data used in analyses were tested for normality using a Shapiro-Wilk test and homogeneity of variance using Levene's test. Subsequently, bathymetry at the position of all 30 tagged harbour porpoises from West Greenland was analysed using a Kruskal-Wallis test followed by a post-hoc Dunn's comparison test, and the dive depth of 2 female harbour porpoises was analysed using a 1-way ANOVA followed by a post hoc Tukey comparison test. Dive depth based on the median was analysed using a Mann-Whitney *U*-test. Student's 2-sample *t*-test was used for comparing travel rate (km d^{-1}) and maximum dive depth of 2 female harbour porpoises when moving inshore and offshore. p-values less than 0.05 are considered significant.

RESULTS

Movement, bathymetry and dive depth

West Greenland harbour porpoises

Thirty satellite tags deployed on harbour porpoises provided information for an average of 250 d (Table 1, range: 16–1047 d, SD = 267) covering a total combined MCP area of 4 144 749 km^2 (Fig. 1). The kernel home range (50%) was concentrated around the continental shelf off West Greenland (Fig. 2). The kernel utilisation range (95%) covered a much larger area including a large part of the North Atlantic. The porpoises tagged in West Greenland were categorised

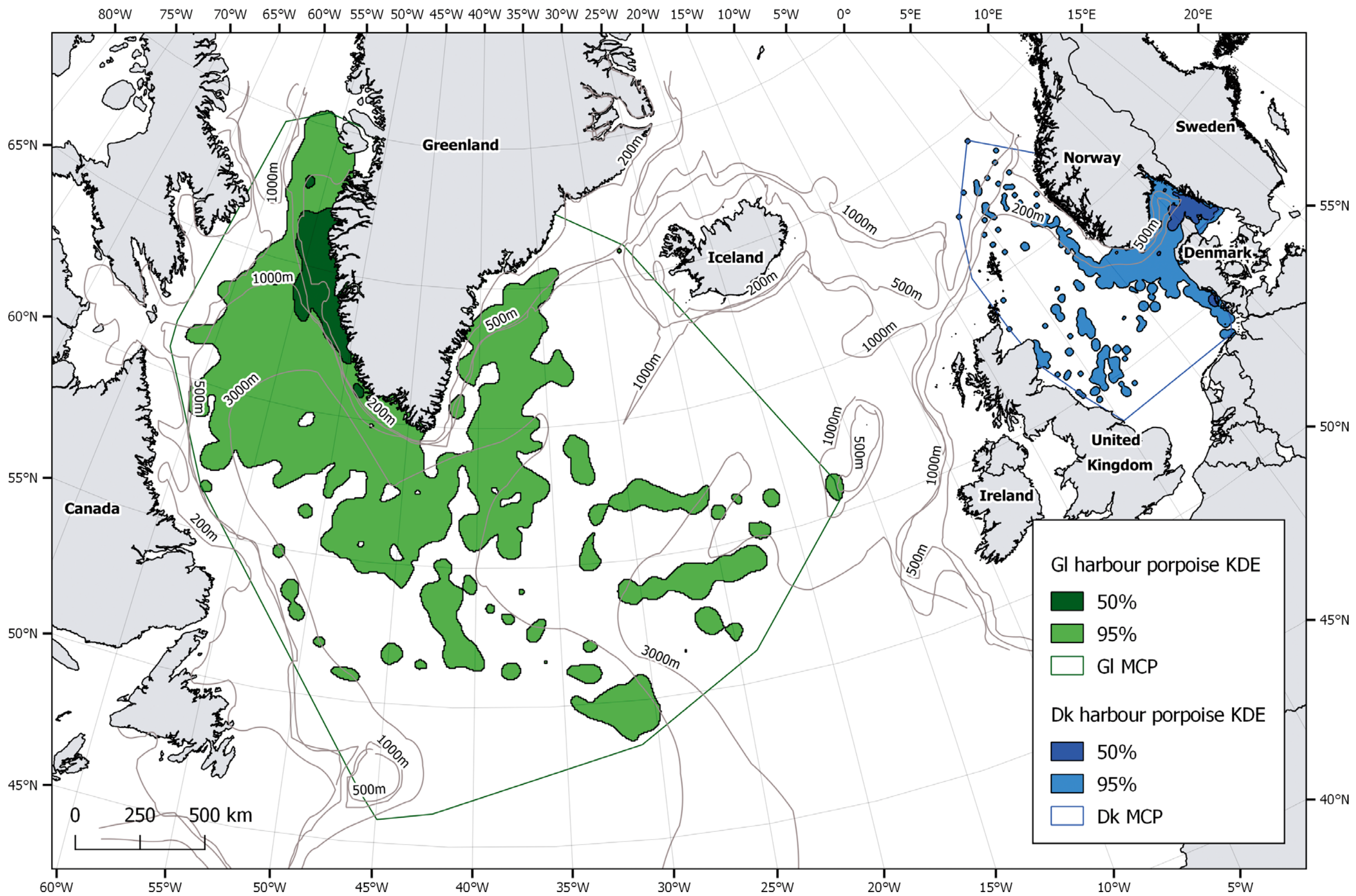

Fig. 2. Heatmaps (QGIS 2.18) for harbour porpoises tagged in Denmark and West Greenland, with kernel home ranges (50%, Gl: dark green, Dk: dark blue) and kernel utilisation range (95%, Gl: green, Dk: blue) and minimum convex polygons (Gl: green, Dk: blue). KDE: kernel density estimate

as being offshore when they had left the continental shelf areas (water depths of <200 m) for 20 out of 30 d. This criterion was developed in order to allow for some temporary crossing of the continental shelf area. Using these criteria, 15 of the porpoises left the West Greenland shelf areas on average 106 d (range: 2–218 d, SD = 91) after deployment: 12 left between October and February, 2 left in July, and 1 left in August. These 15 porpoises (60% females: 1 calf, 5 subadults, and 3 adults, and 40% males: 3 subadults and 3 adults, see Lockyer et al. 2003b for age classification) transmitted for an average of 394 d (range: 29–1047 d, SD = 317) while they moved south or west into deeper waters of Davis Strait, the Labrador Sea and the North Atlantic (Fig. 1). However, none of the porpoises entered the shelf areas of eastern Canada or Iceland. Of the 15 animals that went offshore, 4 ended their transmissions before their winter/spring (January–June) movement could be identified. Of the remaining 11 porpoises, 10 moved to offshore areas in the North Atlantic (defined as being south of 60° N, Fig. 1) throughout winter/spring and went as far south as 45° N and as far west as 18° W, and ended their transmissions on average after 515 d (range: 227–1047 d, SD = 305). The 15 harbour porpoises that remained on the West Greenland shelf areas ended their transmissions in waters off Southwest Greenland or the northeastern part of the Labrador Sea on average after 106 d (range: 16–170 d, SD = 48).

The average water depth within the total range of all porpoises tagged in West Greenland was 2936 m (range: 8–4654 m, SD = 1007); however, the water depth of the areas that the porpoises preferred varied significantly between months (H_{11} = 355.04, $p <$ 0.0001, Fig. 3A). Porpoises moved into areas with deeper water depths in autumn/early winter (average of 2486 m in August–December, SD = 420) compared to winter/early spring (average of 599 m in January–June, SD = 277, $p < 0.0001$).

Two female porpoises (instrumented with SPLASH tags, Table 1) that moved offshore provided a daily maximum dive depth for 104 and 150 d, respectively.

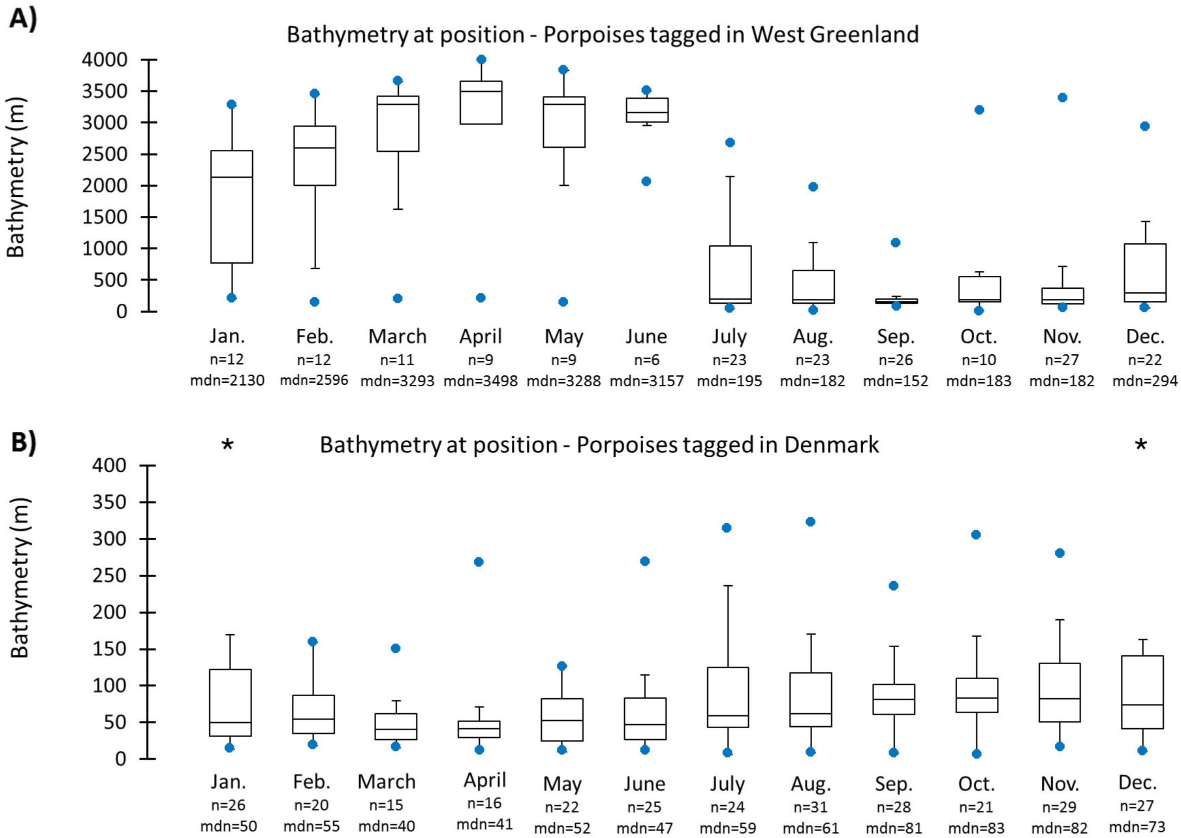

Fig. 3. Preferred monthly average bathymetry for (A) 30 harbour porpoises from West Greenland and (B) for 71 porpoises from the North Sea/Skagerrak. The central horizontal line in the boxes is the median and the lower and upper limits of the box are the first and third quartiles, respectively. The upper and lower bounds of whiskers represent the 95% confidence interval, and blue dots indicate the minimum and maximum bathymetry range for each month. Number of animals (n) and median water depth (mdn) is given for each month. In (B), 2 outliers in January (841 m) and December (658 m) are indicated by asterisks

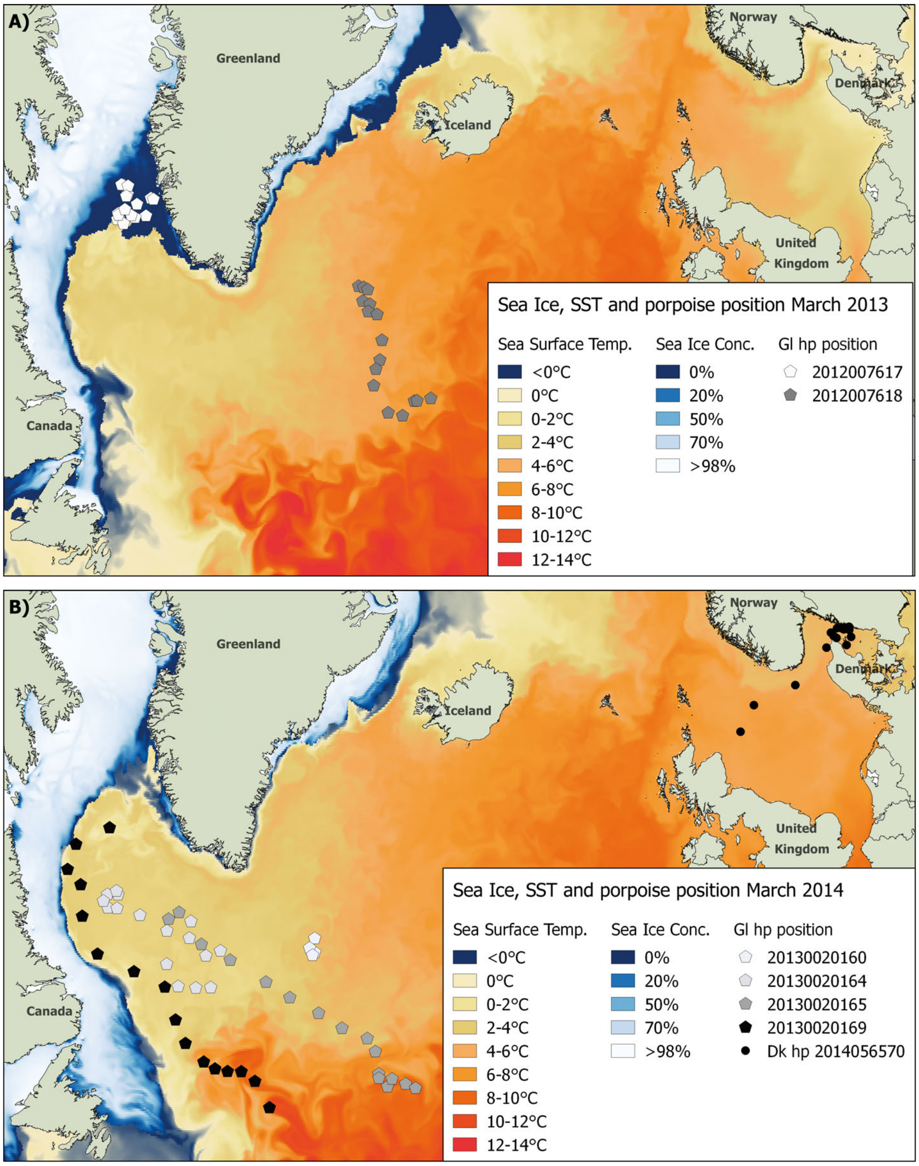

Fig. 4. Average sea ice extent and sea surface temperature (SST) in March in (A) 2013, (B) 2014, (C) 2015 and (D) 2016. Locations obtained from the tagged porpoises in March for these years are shown with dots for animals tagged in both West Greenland and Denmark. The area of 0% sea ice (dark blue) covers the same area as sea ice temperatures <0°C (dark blue)

They dived to a mean daily maximum depth of 252 m (range: 114–410 m, SD = 66, Table 1) with a record deep dive of 410 m. They dived significantly deeper ($F_{11,253}$ = 12.191, p < 0.0001) in November, December, February and March (p < 0.0001) and significantly deeper when moving into offshore waters (p < 0.05).

Maximum dive depth from the Mk10 tags (n = 17) was obtained using the daily maximum depth bin visited by the porpoise (Table 1). The median dive depth of all 17 porpoises was 200 m (range: 50–400 m). Three of the 17 porpoises moved offshore, and their maximum dive depth was significantly shallower when they were offshore than when they were at the shelf areas (150 and 200 m, respectively, Mann-Whitney U = 632.5, p < 0.05, 2-tailed).

The average daily travel rate of all 30 porpoises were significantly different among months ($F_{11,2980}$ = 33.337, p < 0.0001), with higher mean travel rates in March–June (36 km d^{-1}, SD = 26.7, p < 0.0001) compared to the remaining months (22 km d^{-1}, SD = 21.06). The porpoises moved on average twice as fast in June (53 km d^{-1}, SD = 28) than in all other months combined (25 km d^{-1}, SD = 6.5).

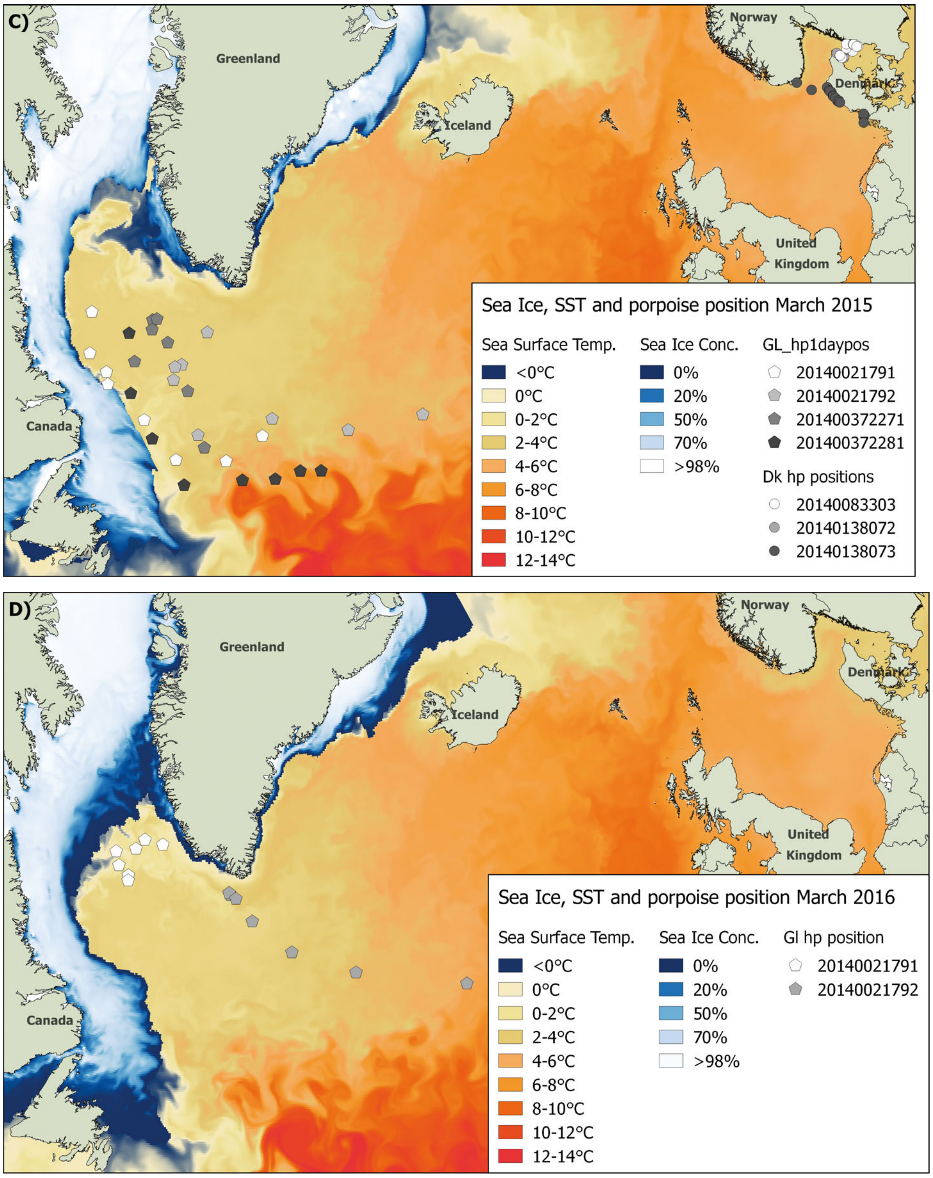

Fig. 4. (continued)

North Sea harbour porpoises

The 71 harbour porpoises instrumented with satellite transmitters in Danish waters provided information for an average of 126 d (range: 5–463 d, SD = 92, Table S1), while covering an MCP area of 588 165 km^2 (Fig. 1). They used most of the Kattegat, Skagerrak and North Sea except for the southern part, but the kernel home range (50 %) was concentrated in the Skagerrak, around Skagen and on the west coast of Denmark (55° N, Fig. 2). The kernel utilisation range (95 %) displayed their use of the North Sea and the east coast of the United Kingdom. One porpoise went north to 64° N and as far west as 3° W, while 4 animals visited fjords in the southern part of Norway (south of 63° N).

The average water depth within the total range of the porpoises tagged in Denmark was 295 m (range: 1–2188 m, SD = 397), and the tagged porpoises showed a preference for areas with an average water depth of 84 m (range: 10–410 m, SD = 69). We found no significant differences in the average bathymetric depths and months in the areas used ($F_{11,272}$ = 1.487, p = 0.136, Fig. 3B). The average daily travel rate was significantly different among months ($F_{11,3292}$ = 2.478, p < 0.004) and lowest in April (15 km d^{-1}, SD = 13.1, p < 0.021) compared to all other months (18 km d^{-1}, SD = 16.0). There were no significant differences (t_{5805}, p = 0.051) in the proportion of months represented in the tagging data from porpoises tagged in Denmark and in West Greenland, thus the travel rates for the 2 areas were compared. When including all months, harbour porpoises from West Greenland had a significantly faster travel rate than porpoises from the North Sea (25 vs. 18 km d^{-1}, t_{5775}, p < 0.0001).

Porpoise distribution in relation to sea ice and SST

The largest extension of sea ice coverage during 2013–2016 in West Greenland occurred in March in all years (Fig. 4), and was used to analyse the distance between porpoises (n = 11) and the sea ice edge. The mean distance from all porpoise positions to the sea ice was 425 km (range: 10–1336 km, SD = 348), and the mean SST at all porpoise positions in March was 3.3°C (range: 2.0–11.5°C, SD = 2.91). No sea ice was present in March in the areas frequented by the North Sea porpoises, and mean SST was 4.6°C (range: 5.1–6.9°C, SD = 0.89).

Philopatry

Six of the 15 porpoises from West Greenland that moved offshore (2 adult and 2 subadult females, and 1 adult and 1 subadult male) returned within 50 km of their tagging position after a mean of 490 d after tagging (range: 344–741, SD = 193). Five of these returned the following summer (July–August, after a mean of 366 d after tagging), and 1 subadult male porpoise returned to West Greenland in July 2016, 2 yr after deployment, after visiting the East Greenland shelf during July 2015 in the first year after instrumentation. Another offshore male porpoise made extensive movements in the North Atlantic (as far east as 22° W) before returning to West Greenland 737 d after tagging. This male left the tagging area for a second time, in October, 81 d upon its latest arrival. The remaining 9 porpoises did not return to the tagging area, but ended their transmissions after a mean of 211 d (range: 29–487, SD = 155). Seven of the 9 porpoises ended their transmissions between October and March (29–268 d after instrumentation). One of the 9 porpoises (subadult male) arrived at the East Greenland shelf areas in September 2015, 1 yr after instrumentation, where it stayed until contact with the tag was lost in November 2015. The last of the 9 porpoises commenced its return to West Greenland at 50° N, but ended the transmissions ~300 km before reaching the tagging area.

Six male porpoises (5 subadults and 1 adult) from the North Sea returned within 50 km of their tagging position in March (April–June), on average 372 d after tagging (range: 300–461 d, SD = 59). The remaining 65 porpoises transmitted for a mean 42 d (range: 1–215 d, SD = 35).

DISCUSSION

This study is the first to document harbour porpoises leaving shelf areas to conduct large-scale wintering movements over deep waters in the North Atlantic, where some moved as far east as 18° W (more than 2000 km from the tagging area). The porpoises tagged in West Greenland used an area 7.5 times larger than the area used by porpoises from the North Sea. Both the scale of the movements and the seasonal selection of offshore habitats are evidently different from what is typical for tracked porpoises in the North Sea or the Northwest Atlantic, which move in more focal areas (Read & Westgate 1997, Johnston et al. 2005). Due to their size and limited capacity for energy storage, harbour porpoises are believed to spend the majority of their time locating suitable prey items; thus their movement is most likely a direct consequence of the location of preferred prey (Gannon et al. 1998, Sveegaard et al. 2015, Wisniewska et al. 2016, 2018). In winter, when the sea ice covers the majority of the Davis Strait and parts of the Labrador Sea, porpoises are forced to abandon the shelf areas of West Greenland until spring, when the winter sea ice retreats. This retrieval triggers a large bloom of primary production that attracts high densities of phytoplankton-foraging fish and zooplankton (Bluhm & Gradinger 2008) on which West Greenland porpoises and other cetaceans forage.

This study has documented an impressive seasonal movement of harbour porpoises from West Greenland which has not previously been reported for porpoises, although it has been suggested that the Gulf of Maine/Bay of Fundy porpoise population has the capacity to make extensive offshore winter movements in order to follow their prey (Read & Gaskin 1985, Palka et al. 1996, Read et al. 1996). This might also be true for other porpoise populations, and the lack of documented offshore sightings of porpoises in the North Atlantic may be due to lack of long-term tracking studies and a seasonal mismatch in survey coverage and porpoise distribution. Surveys for harbour porpoises in the North Atlantic have always been conducted during summer, at which time porpoises are located in shelf waters as indicated by this study (in particular in July and August, see Fig. 1); thus there have been no observations of their winter distribution. Satellite telemetry offers a unique possibility for studying movements and behaviour of species that are overlooked due to their cryptic nature, such as harbour porpoises.

The porpoises tagged in Danish waters were instrumented with satellite transmitters designed to detach by using iron nuts that corrode with time (Teilmann et al. 2007, Sveegaard et al. 2011). This could potentially have caused the tags to detach before the batteries were drained, consequently providing less information. In West Greenland, stainless steel nuts were used to obtain data on inter-annual movements. Some of the tags attached to porpoises in West Greenland provided a record duration of 1047 d and provided novel insight into porpoise movements over several years, revealing their affiliation to the shelves of Greenland.

The harbour porpoises from West Greenland that transmitted during winter/spring moved into offshore areas with significantly greater water depths than where they spend the summer/autumn. This is in contrast to the North Sea porpoises, which showed no seasonal selection of areas with specific water depths (Fig. 3). This is probably due to general availability of ice-free shallow water depths in the North Sea that allow the porpoises to forage on both pelagic and benthic species, providing a larger prey base with less need for extensive movements.

There are no records of harbour porpoises being present in areas with sea ice formation, and their small size and dorsal fin probably makes them vulnerable to ice; however, harbour porpoises in West Greenland seem unaffected by negative SST and were distributed as close as 10 km from the sea ice. In general, the distance of porpoises to the sea ice varied greatly in this study; some animals were distributed close to the edge of the sea ice but never inside areas with ice, while others moved away and went south into the North Atlantic (Fig. 4). The SSTs used by the porpoises from West Greenland (−2 to 11.5°C) suggest a large tolerance towards a wide range of SSTs rather than having a preferred SST, which is in contrast to the study by Wingfield et al. (2017).

Two female porpoises tagged in West Greenland showed the capacity to perform deep dives (390 and 410 m, respectively) to nearly twice the maximum depths previously reported for harbour porpoises (Westgate et al. 1995, Teilmann et al. 2007). This suggests that harbour porpoises from West Greenland are specialised in using a different niche than other harbour porpoise populations, and they probably rely on mesopelagic prey resources. Little is known about the mesopelagic community in offshore waters, despite the large estimated fish biomass (St. John et al. 2016), but it is likely that the harbour porpoises from West Greenland target this zone during winter. This is further supported by the binned maximum dive depths (Mk10 tags) that indicate the potential for harbour porpoises reaching the mesopelagic layer at 200 m, and also by findings of vertically migrating lanternfish in the stomachs of West Greenland porpoises (Heywood 1996, Heide-Jørgensen et al. 2011). In addtion, findings of several mesopelagic species in the stomach of an immature male porpoise bycaught in an offshore driftnet on the US east coast support this hypothesis (Read et al. 1996).

Porpoises wintering in the North Atlantic and perhaps also in West Greenland are likely adapted to deal with larger spatial dispersal and more dynamic behaviour of high-quality prey species, which require more extensive movements compared to Northeast Atlantic porpoises. This suggests that porpoises from West Greenland in comparison to porpoises from the North Sea are challenged by a more geographically dispersed prey field, both vertically and horizontally. This is supported by the higher daily travel rate in porpoises from West Greenland in the months when they are present in offshore waters (Fig. 3A). The travel rate of porpoises from the North Sea is within the range for porpoises located on shelf areas in West Greenland, whereas the larger daily travel rate covering larger areas for offshore porpoises suggests that these porpoises are more challenged in their search for prey and therefore have a larger daily search radius. The lower travel rate seen in April for the North Sea porpoises probably reflects less intensive foraging in this period where the water starts warming up and the animals need less energy, or potentially caused by a seasonal shift in prey as seen in other porpoise populations (Gannon et al. 1998, Víkingsson et al. 2003).

Porpoises in Greenland mate and give birth during summer (Lockyer et al. 2003b), and site fidelity is an important driver for the porpoises, as demonstrated in our study. This is supported by a subadult male porpoise (PTT ID 372281, Table 1) that spent the first post-deployment summer (July) in East Greenland, but returned to West Greenland for the second summer (July +1 yr), where it presumably became sexually mature (at ca. 127 cm according to Lockyer et al.

2001). This is also reflected in the kernel density estimations, where the 50% core area is at the shelves off Greenland (Fig. 2). Offshore porpoises are all moving in areas with deep waters in May and start returning to West Greenland in June and July, and in August, most porpoise positions are located in either East or West Greenland (Fig. 1). This could also explain why the porpoises moved nearly twice as fast in June compared to all other months as they returned to West Greenland to reproduce.

Fifty percent (n = 15) of the porpoises tagged in West Greenland moved offshore after an average of 106 d; however, sex and length of the remaining 15 animals that stayed in the continental shelf area did not indicate any segregation in behaviour that could explain their avoidance of offshore areas. Rather, the remaining porpoises probably did not transmit long enough to document offshore movement, as seen for the 8 tags with defective batteries that reduced the longevity of the tag.

In order to identify the movement potential and site fidelity to the summer feeding grounds of harbour porpoises from West Greenland, the tag has to transmit for at least 2 yr, as some animals did not return to West Greenland until >700 d after deployment. However, this may be due to the animal being immature during the second summer and therefore not needing to return to West Greenland to reproduce until the third summer.

This study demonstrates that the population of harbour porpoises in West Greenland disperses wider than other harbour porpoise populations for which movements have previously been studied. Harbour porpoises from West Greenland are capable of inhabiting deep oceanic waters of the North Atlantic and perform deep dives. The tracking also indicates that despite having wide-ranging dispersal capability, harbour porpoises with transmitters lasting >1 yr exhibited site fidelity to specific summer feeding grounds, as also suggested by Read & Westgate (1997) for harbour porpoises in Canadian waters, and seen in porpoises from the North Sea (this study). Five of the 6 porpoises that returned to West Greenland and to the very same place where they were tagged, were presumed to be sexually mature (PTT ID 21791 was 111 cm when tagged and could most likely not have reached sexual maturity upon its return, 344 d after deployment), which suggests that this area is an important feeding, breeding and mating ground during summer and fall.

Site fidelity to the summering area explains the genetic and morphometric differentiation of the West Greenland population from other harbour porpoise populations in the North Atlantic (Andersen et al. 2001, Tolley et al. 2001, Huggenberger et al. 2002). However, independent of the genetic differentiation, the West Greenland porpoises also display ecological specialisations compared to other studied harbour porpoise populations (Fontaine et al. 2014) by displaying a large prey diversity (Heide-Jørgensen et al. 2011) and different migratory and diving behaviour, all characteristics suggesting that harbour porpoises from West Greenland belong to a unique oceanic ecotype.

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LITERATURE CITED

Andersen LW (2003) Harbour porpoises (*Phocoena phocoena*) in the North Atlantic: distribution and genetic population structure. NAMMCO Sci Publ 5:11–29

Andersen LW, Ruzzante DE, Walton M, Berggren P, Bjørge A, Lockyer C (2001) Conservation genetics of harbour porpoises, *Phocoena phocoena*, in eastern and central North Atlantic. Conserv Genet 2:309–324

Andreasen H, Ross SD, Siebert U, Andersen NG, Ronnenberg K, Gilles A (2017) Diet composition and food consumption rate of harbor porpoises (*Phocoena phocoena*) in the western Baltic Sea. Mar Mamm Sci 33:1053–1079

Bluhm BA, Gradinger R (2008) Regional variability in food availability for Arctic marine mammals. Ecol Appl 18: S77–S96

Danish Meteorological Institute (2017) Ice charts. www.dmi.dk/hav/groenland-og-arktis/iskort/

Douglas D (2006) The Douglas Argos-Filter Algorithm, version 7.03. https://alaska.usgs.gov/science/biology/spatial/manual.html

Edrén S, Wisz MS, Teilmann J, Dietz R, Söderkvist J (2010) Modelling spatial patterns in harbour porpoise satellite telemetry data using maximum entropy. Ecography 33: 698–708

Fontaine PM, Hammill MO, Barrette C, Kingsley MC (1994) Summer diet of the harbour porpoise (*Phocoena phocoena*) in the estuary and the northern Gulf of St. Lawrence. Can J Fish Aquat Sci 51:172–178
Fontaine MC, Roland K, Calves I, Austerlitz F and others (2014) Postglacial climate changes and rise of three ecotypes of harbor porpoises, *Phocoena phocoena*, in western Palearctic waters. Mol Ecol 23:3306–3321
Forney KA, Barlow J (1998) Seasonal patterns in the abundance and distribution of California cetaceans, 1991–1992. Mar Mamm Sci 14:460–489
Freitas C, Lydersen C, Fedak MA, Kovacs KM (2008) A simple new algorithm to filter marine mammal Argos locations. Mar Mamm Sci 24:315–325
Gannon D, Craddock JE, Read AJ (1998) Autumn food habits of harbor porpoises, *Phocoena phocoena*, in the Gulf of Maine. Fish Bull 96:428–437
Gilles A, Adler S, Kaschner K, Scheidat M, Siebert U (2011) Modelling harbour porpoise seasonal density as a function of the German Bight environment: implications for management. Endang Species Res 14:157–169
Hammond PS, Macleod K, Berggren P, Borchers DL and others (2013) Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. Biol Conserv 164:107–122
Hansen RG, Heide-Jørgensen MP (2013) Spatial trends in abundance of long-finned pilot whales, white-beaked dolphins and harbour porpoises in West Greenland. Mar Biol 160:2929–2941
Hansen RG, Boye TK, Larsen RS, Nielsen NH and others (in press) Abundance of whales in West and East Greenland in summer 2015. NAMMCO Sci Publ
Heide-Jørgensen MP, Iversen M, Nielsen NH, Lockyer C, Stern H, Ribergaard MH (2011) Harbour porpoises respond to climate change. Ecol Evol 1:579–585
Heywood KJ (1996) Diel vertical migration of zooplankton in the Northeast Atlantic. J Plankton Res 18:163–184
Huggenberger S, Benke H, Kinze C (2002) Geographical variation in harbour porpoise (*Phocoena phocoena*) skulls: support for a separate non-migratory population in the Baltic proper. Ophelia 56:1–12
Jakobsson M, Mayer LA, Coakley B, Dowdeswell JA and others (2012) The International Bathymetric Chart of the Arctic Ocean (IBCAO), Version 3.0. Geophys Res Lett 39: L12609
Johnston DW, Westgate AJ, Read AJ (2005) Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy. Mar Ecol Prog Ser 295: 279–293
Kie JG (2013) A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. Anim Biotelem 1:13
Kleiber M (1947) Body size and metabolic rate. Physiol Rev 27:511–541
Koopman HN (1998) Topographical distribution of the blubber of harbor porpoises (*Phocoena phocoena*). J Mammal 79:260–270
Leopold MF, Begeman L, Heße E, van der Hiele J, and others (2015) Porpoises: from predators to prey. J Sea Res 97: 14–23
Lockyer C, Heide-Jørgensen MP, Jensen J, Kinze CC, Sørensen TB (2001) Age, length and reproductive parameters of harbour porpoises *Phocoena phocoena* (L.) from West Greenland. ICES J Mar Sci 58:154–162
Lockyer C, Desportes G, Hansen K, Labberté S, Siebert U (2003a) Monitoring growth and energy utilisation of the harbour porpoise (*Phocoena phocoena*) in human care. NAMMCO Sci Publ 5:107–120
Lockyer C, Heide-Jørgensen MP, Jensen J, Walton MJ (2003b) Life history and ecology of harbour porpoises (*Phocoena phocoena*) from West Greenland. NAMMCO Sci Publ 5:177–194
NAMMCO (North Atlantic Marine Mammal Commission) (2013) North Atlantic Marine Mammal Commission Annual Report 2013. Scientific committee working group on harbour porpoises, Tromsø
Palka D, Read A, Westgate A, Johnston D (1996) Summary of current knowledge of harbour porpoises in US and Canadian Atlantic waters. Rep Int Whaling Comm 46: 559–566
QGIS Development Team (2017) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.org
R Development Core Team (2008) R: a language and environment for statistical computing. www.R-project.org
Read AJ, Gaskin D (1985) Radio tracking the movements and activities of harbor porpoises, *Phocoena phocoena* (L.), in the Bay of Fundy, Canada. Fish Bull 83: 543–552
Read AJ, Hohn AA (1995) Life in the fast lane: the life history of harbor porpoises from the Gulf of Maine. Mar Mamm Sci 11:423–440
Read A, Westgate A (1997) Monitoring the movements of harbour porpoises (*Phocoena phocoena*) with satellite telemetry. Mar Biol 130:315–323
Read AJ, Nicolas JR, Craddock JE (1996) Winter capture of a harbor porpoise in a pelagic drift net off North Carolina. Fish Bull 94:381–383
Rosel P, Tiedemann R, Walton M (1999) Genetic evidence for limited trans-Atlantic movements of the harbor porpoise *Phocoena phocoena.* Mar Biol 133:583–591
Santos M, Pierce G (2003) The diet of harbour porpoise (*Phocoena phocoena*) in the northeast Atlantic. Oceanogr Mar Biol Annu Rev 41:355–390
Spitz J, Trites AW, Becquet V, Brind'Amour A, Cherel Y, Galois R, Ridoux V (2012) Cost of living dictates what whales, dolphins and porpoises eat: the importance of prey quality on predator foraging strategies. PLOS ONE 7:e50096
St. John MA, Borja A, Chust G, Heath M and others (2016) A dark hole in our understanding of marine ecosystems and their services: perspectives from the mesopelagic community. Front Mar Sci 3:31
Sveegaard S, Teilmann J, Tougaard J, Dietz R, Mouritsen KN, Desportes G, Siebert U (2011) High-density areas for harbor porpoises (*Phocoena phocoena*) identified by satellite tracking. Mar Mamm Sci 27:230–246
Sveegaard S, Galatius A, Dietz R, Kyhn L and others (2015) Defining management units for cetaceans by combining genetics, morphology, acoustics and satellite tracking. Glob Ecol Conserv 3:839–850
Teilmann J, Dietz R (1998) Status of the harbour porpoise in Greenland. Polar Biol 19:211–220
Teilmann J, Larsen F, Desportes G (2007) Time allocation and diving behaviour of harbour porpoises (*Phocoena phocoena*) in Danish and adjacent waters. J Cetacean Res Manag 9:201–210
Tolley KA, Víkingsson GA, Rosel PE (2001) Mitochondrial DNA sequence variation and phylogeographic patterns

in harbour porpoises (*Phocoena phocoena*) from the North Atlantic. Conserv Genet 2:349–361

Víkingsson GA, Ólafsdóttir D, Sigurjónsson J (2003) Geographical, and seasonal variation in the diet of harbour porpoises (*Phocoena phocoena*) in Icelandic coastal waters. NAMMCO Sci Publ 5:243–270

Westgate AJ, Head AJ, Berggren P, Koopman HN, Gaskin DE (1995) Diving behaviour of harbour porpoises, *Phocoena phocoena*. Can J Fish Aquat Sci 52:1064–1073

Wingfield JE, O'Brien M, Lyubchich V, Roberts JJ, Halpin PN, Rice AN, Bailey H (2017) Year-round spatiotemporal distribution of harbour porpoises within and around the Maryland wind energy area. PLOS ONE 12: e0176653

Wisniewska DM, Johnson M, Teilmann J, Rojano-Doñate L and others (2016) Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. Curr Biol 26:1441–1446

Wisniewska DM, Johnson M, Teilmann J, Rojano-Donate L, and others (2018) Response to 'Resilience of harbor porpoises to anthropogenic disturbance: Must they really feed continuously?' Mar Mamm Sci 34:265–270

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