ARCTIC
VOL. 65, NO. 1 (MARCH 2012) P. 76–86

Lost Highway Not Forgotten: Satellite Tracking of a Bowhead Whale (*Balaena mysticetus*) from the Critically Endangered Spitsbergen Stock

CHRISTIAN LYDERSEN,[1,2] CARLA FREITAS,[1] ØYSTEIN WIIG,[3] LUTZ BACHMANN,[3] MADS PETER HEIDE-JØRGENSEN,[4] RENÉ SWIFT[5] and KIT M. KOVACS[1]

(*Received 11 April 2011; accepted in revised form 30 May 2011*)

ABSTRACT. The Spitsbergen bowhead whale stock is critically endangered. It is believed to number in the tens. Here we report results from the first satellite transmitter ever deployed on an individual from this stock. A female whale was tagged on 3 April 2010 (at 79˚54′ N, 01˚03′ E), but no locations were transmitted by the tag until 30 April 2010, after which data were received continuously for 86 days. Additionally, three small clusters of locations were transmitted later in the year; the latest was received 20 December 2010 (262 days after deployment). During the 86 days of continuous tracking, the whale initially remained in the middle of the Fram Strait, between 77˚45′ N, 5˚ W and 80˚10′ N, 5˚ E. For a two-week period starting around 10 June 2010, the whale traveled southwest down to 73˚40′ N (at least 950 km). Subsequently it remained at southern latitudes between ~70˚ and 73˚ N until the tag stopped continuous transmissions on 24 July. Movement patterns analyzed using first-passage times (FTP), fitted as functions of various environmental variables using Cox Proportional Hazards models, showed that the whale spent most of its time in waters close to the ice edge with modest ice coverage, over areas where the bottom slope was relatively steep. Winter positions (27 November–20 December 2010) revealed that the whale was back in the North at about 80˚ N. This information, in combination with recent data from passive acoustic listening devices, suggests that the Spitsbergen bowhead stock overwinters at high-latitude locations. The north-south movements of this whale during summer are consistent with the patterns that early whalers described for bowhead whales in this region in the 16th and 17th centuries.

Key words: bowhead whale, *Balaena mysticetus*, satellite tracking, habitat use, first-passage time

RÉSUMÉ. La population de baleines boréales de Spitzberg est en danger critique d'extinction. L'on croit qu'elle se chiffrerait dans la dizaine. Ici, nous faisons état des résultats obtenus à l'aide du premier émetteur satellite à n'avoir jamais été installé sur un individu de cette population. Une baleine femelle a été marquée le 3 avril 2010 (à 79˚54′ N, 01˚03′ E), mais aucun signal n'a été transmis par ce marquage avant le 30 avril 2010, après quoi nous avons reçu des données continuelles pendant 86 jours. Plus tard dans le courant de l'année, nous avons également reçu trois petits blocs d'information, dont le dernier a été transmis le 20 décembre 2010 (262 jours après la date du marquage). Au cours des 86 jours d'information continuelle, la baleine restait d'abord au milieu du détroit de Fram, entre 77˚45′ N, 5˚ O et 80˚10′ N, 5˚ E. Pendant une période de deux semaines commençant vers le 10 juin 2010, la baleine s'est déplacée vers le sud-ouest jusqu'à 73˚40′ N (au moins 950 km). Par la suite, elle est restée dans les latitudes du sud entre ~70˚ et 73˚ N jusqu'à ce que le marquage cesse les transmissions continuelles le 24 juillet. Les habitudes de déplacement analysées en recourant aux temps du premier passage (FTP), ajustées à titre de fonctions de diverses variables environnementales s'appuyant sur les modèles des hasards proportionnels de Cox, ont laissé entrevoir que la baleine passait la plus grande partie de son temps dans les eaux à proximité des lisières de glace dont la couverture était modeste par rapport aux endroits où la pente du fond était relativement abrupte. Les positions enregistrées en hiver (du 27 novembre au 20 décembre 2010) ont révélé que la baleine était retournée dans le nord à environ 80˚ N. Cette information, alliée aux récentes données provenant d'appareils d'écoute acoustique, suggère que la population de baleines boréales de Spitzberg passe l'hiver à de hautes latitudes. Pendant l'été, les mouvements nord-sud de cette baleine sont conformes aux habitudes de déplacement de la baleine boréale, telles que décrites par les anciens baleiniers dans cette région au cours des XVI[e] et XVII[e] siècles.

Mots clés : baleine boréale, *Balaena mysticetus*, repérage par satellite, utilisation de l'habitat, temps du premier passage

Traduit pour la revue *Arctic* par Nicole Giguère.

[1] Norwegian Polar Institute, N-9296 Tromsø, Norway
[2] Corresponding author: lydersen@npolar.no
[3] National Centre for Biosystematics, Natural History Museum, University of Oslo, N-0318 Oslo, Norway
[4] Greenland Institute of Natural Resources, Kivioq 2, DK-3900 Nuuk, Greenland
[5] Sea Mammal Research Unit, Scottish Oceans Institute, Gatty Marine Laboratory, School of Biology, University of St. Andrews, St. Andrews, Fife KY16 8LB, UK

INTRODUCTION

The bowhead whale (*Balaena mysticetus*) is an endemic Arctic species that is generally found in close association with sea ice. With its thick blubber layer (up to 50 cm) and a bulky shape that reduces its surface-to-volume ratio, this species is well adapted to living in cold Arctic waters year-round. Bowheads are relatively slow swimmers that feed by filtering zooplankton out of engulfed water masses with their 4.5 – 5 m long baleen plates. The species was very attractive for early whalers; bowheads were valued both for their baleen and for the oil content of their huge blubber deposits, which had the added advantage of making them float when killed. Starting in the mid 1500s, the Basques, who were subsequently joined by other peoples, hunted stock after stock of bowhead whales to near-extinction (Woodby and Bodkin, 1993). The largest of these stocks was the Spitsbergen stock, found in an area that extends eastward from East Greenland and includes the Greenland, Barents, and Kara seas. This stock was estimated to consist of 25 000 – 100 000 whales before the exploitation started in 1611 (Allen and Keay, 2006) in the Svalbard area. Within a century, this stock was more or less exhausted. A recent compilation of sightings of bowhead whales from the Svalbard area between 1940 and 2009 documented only three sightings before 1980, but 43 sightings in the following 29 years (Wiig et al., 2010a). Similar findings are reported from Northeast Greenland, with three observations between 1940 and 1979 and 20 observations between 1980 and 2004 (Gilg and Born, 2005). It is unknown whether this increase in sightings is due to increased abundance of the whales or to the large increase in tourist ships and recent establishment of a cetacean-sighting program.

While the Spitsbergen stock today is believed to number in the tens (Wiig et al., 2010a) and is considered critically endangered by the International Union of Conservation of Nature (IUCN) (Reilly et al., 2008), bowheads in the three other recognized stocks (Givens et al., 2010) are more numerous. The Bering-Chukchi-Beaufort seas stock is estimated to be close to 10 500 individuals (George et al., 2004; Gerber et al., 2007), and a recent negatively biased abundance estimate for the Eastern Canada – West Greenland stock indicated a number close to 6300 (IWC, 2010). The Okhotsk Sea stock, the smallest of these other stocks, consisted of some 3000 individuals in pre-whaling times. Its current status is not known, though a minimum abundance estimate of 247 whales has been reported (IWC, 2010).

Knowledge about movement patterns of bowhead whales stems primarily from the two most numerous stocks and is based on aerial surveys and satellite tracking. The general pattern that emerges from these studies is that the whales follow the receding ice edge northwards during summer and then south again when the ice forms during the late fall and early winter (e.g., Heide-Jørgensen et al., 2006; Quakenbush et al., 2010). During the summer, bowhead whales feed extensively, generally in shallow areas (Krutzikowsky and Mate, 2000; Heide-Jørgensen et al., 2003; Laidre et al., 2007) with many of their foraging dives targeting the bottom (Laidre et al., 2007, 2010). Large concentrations of zooplankton can often be found in such benthic environments (Laidre et al., 2007). Bowhead whales move from one foraging area to another, sometimes crossing deep ice-filled waters, where they apparently do not feed, to reach another shallow foraging area (Heide-Jørgensen et al., 2003). A detailed study of bowhead whale movement with special emphasis on association with sea ice, conducted on the Eastern Canada – West Greenland stock (Ferguson et al., 2010a), found that in winter those whales selected areas close to the maximum ice extent with relatively low ice coverage, thin ice, and small floes, while in summer they selected higher ice coverage and thicker ice with larger floes. The winter habitat selection was presumed to reduce the risk of entrapment, while the summer habitat selection was hypothesized to be related to reduction of killer whale (*Orcinus orca*) predation.

Collective knowledge from centuries of whaling, documented in ships' logs, has suggested that the whales from the Spitsbergen stock move from the north towards the southwest as summer proceeds (Southwell, 1898; Gray, 1931). Generally, bowhead whaling started in May at the ice edge, around the "Northern Whaling Ground" (~77˚ – 80.5˚ N) and ended in August at latitudes as low as 70˚ – 71˚ N in the "Southern Whaling Ground" (~70˚ – 75.5˚ N). These data suggest that bowheads of the Spitsbergen stock display a seasonal movement pattern opposite to those that have been revealed by satellite tracking of other bowhead whale stocks (Heide-Jørgensen et al., 2006; Quakenbush et al., 2010). No movement or habitat selection studies have been conducted on bowhead whales from the critically endangered Spitsbergen stock (for lack of study animals if for no other reason). Here we present the first satellite-tracking data for a whale from this stock and investigate the whale's use of space by examining its movements in relation to various environmental parameters.

MATERIAL AND METHODS

Using the Norwegian Polar Institute's research vessel *Lance* as a working platform, we searched for bowhead whales along the southern ice edge in the Fram Strait (79˚ – 81˚ N, 3˚ W – 24˚ E) between 29 March and 14 April 2010. During all light hours (~0800 to 2000), in addition to having at least two observers with binoculars actively searching for whales, we conducted continuous acoustic monitoring with a towed hydrophone array (or, when passing through ice-filled waters, with sonobuoys). We surveyed a total of 3616 km of track-line during the 19 days at sea.

We observed bowhead whales on two occasions but never detected acoustic signals from this species. The first sighting occurred at 79˚54′ N, 01˚03′ E on 3 April and the second at 80˚30′ N, 02˚0′ E on 13 April. During the first encounter, we found the whale in dense pack ice (water depth 2300 m). Because of the ice situation, we could not use small boats to approach the animal, so we drew near slowly with *Lance* (60.8 m long, 1334 br. reg. tons). This approach was successful, and a satellite transmitter (Spot5, Wildlife Computers) was deployed using an ARTS (Aerial Rocket Transmitter System, Heide-Jørgensen et al., 2001) air gun (12 bar pressure from a distance of about 5 m). The tag was programmed to make 250 transmissions per day between 0800 and 2000 GMT. A skin biopsy was collected at the time of tag deployment using a crossbow with custom-made darts (Palsbøll et al., 1991). This biopsy was used for a molecular sex determination using a PCR-based approach described by Palsbøll et al. (1992) with some modifications (see Heide-Jørgensen et al., 2010). It will also be used for population genetic studies not reported here. The whale was estimated to be about 15 m long. The second bowhead whale we encountered turned out to be the same individual we had observed on 3 April, identified by distinct scarring patterns on the head. Because the transmitter had apparently failed, we attempted to deploy a second satellite tag on the whale. However, the whale did not let us get close enough to attempt a shot. On 30 April, the original satellite tag started to transmit positions, and it continued to do so regularly until 24 July. We also received three small clusters of positions on 27 November, 13 December, and 20 December.

The location data that were received from Argos for the continuous tracking period from 30 April until 24 July were filtered using the argosfilter package in R (R development Core Team, 2010, see Freitas et al., 2008a). We used a maximum speed of 3 m/s, which was based on swimming speed information obtained in previous studies (Zeh et al., 1993; Mate et al., 2000; Heide-Jørgensen et al., 2003; Quakenbush et al., 2010).

In order to quantify habitat use for the tracked whale, we calculated first-passage times (FPTs, Fauchald and Tveraa, 2003) at 5 km intervals, linearly interpolated along the original track. Filtered locations were spaced at median distances of 3.0 km (1st–3rd quartiles were 1.4–5.5 km) and thus had a finer resolution than new, interpolated locations. Note that equally spaced locations are needed in FPT analysis in order to estimate the radius at which animals concentrate their time (Fauchald and Tveraa, 2003). We calculated FPTs for radii ranging from 1 km to 200 km, at 1 km increments. The variance of log(FPT) was then plotted as a function of radii, in order to find the radius of maximum variance, which was then explored using a variety of covariates. The peak variances of log(FPT) occurred at 10 and 45 km (Fig. 1), indicating that the bowhead whale concentrated its time at two spatial scales. FPTs at the larger scale (45 km) were used to investigate how large-scale habitat use intensity was affected by environmental conditions. This was done by fitting these FPTs as a function of various environmental conditions using Cox Proportional Hazards models, following Freitas et al. (2008b). FPTs at 45 km intervals (instead of the original 5 km intervals) were used in order to avoid pseudo-replication of the data. Seven environmental variables were used: Depth (DEP), sea bottom slope (SLO), sea-ice concentration (ICE), distance to the ice (DIST_ICE), chlorophyll-a concentration (CHL), sea surface temperature (SST), and distance to a sea surface temperature front (DIST_F) (Table 1). We extracted all of these variables for the FPT locations using ArcInfo (ESRI, Inc.), MGET (Roberts et al., 2010) and Matlab (The MathWorks™). Model fitting was done in R, using the package Survival. Model selection was done using forward-selection based on the AIC_c (Akaike's Information Criterion, corrected for effective sample size, Burnham and Anderson, 2002). AIC weights (w_i) were used to assess the relative weight of evidence for each model. A model whose weight approaches 1 (e.g., ≥ 0.90) is unambiguously supported by the data, and models with approximately equal weights have a similar level of support (see Burnham and Anderson, 2002; Johnson and Omland, 2004). In this study, five models had weights of 0.90 or greater (Table 2). Averaged coefficients from these five models were therefore used instead of the coefficients of a single best model (Tables 2 and 3), following the recommendations of Burnham and Anderson (2002). Unconditional variance and confidence intervals of these coefficients were also obtained, following Burnham and Anderson (2002).

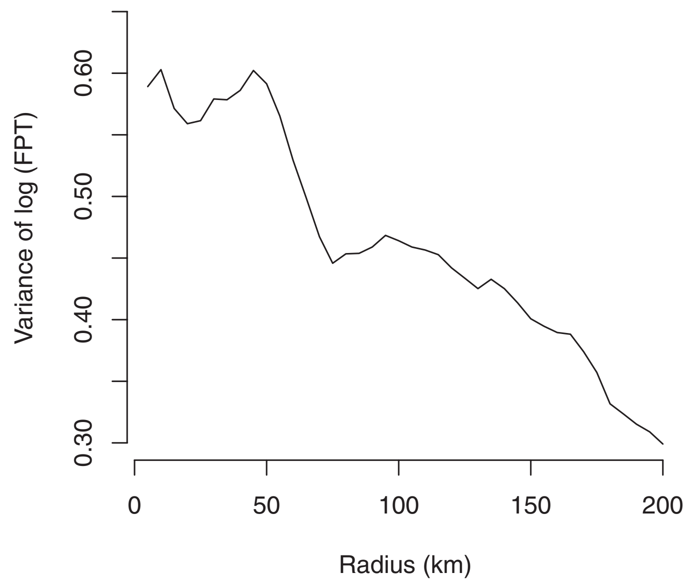

FIG. 1. Variance of log-transformed first-passage time (FPT) as a function of spatial scale. Peaks in variance occurred at radii of 10 and 45 km.

RESULTS

The tagged and biopsied bowhead whale was genetically determined to be a female. Position data were reported for the first time by Argos on 30 April 2010, 27 days after deployment of the tag. The first position was at 79˚46′ N, 01˚34′ E, about 20 km southeast of the tagging location (Fig. 2). The tag transmitted location data continuously for almost three months (86 days) before it paused. At that time, we assumed that it had fallen off the whale. Surprisingly, however, it resumed transmitting for short periods

TABLE 1. Ocean data used for first-passage time modeling.

Variable	Abbreviation	Units	Source
Depth	DEP	m	IBCAO, version 2.0 (see Jakobsson et al., 2008). Pixel resolution is 2 km.
Sea-bottom slope	SLO	%	Calculated from DEP, using ArcInfo (ESRI, Inc.).
Sea-ice concentration	ICE	%	Daily 10 km resolution data from the Ocean and Sea Ice Satellite Application Facility (www.osi-saf.org/).
Distance to the ice[1]	DIST_ICE	km	Calculated from ICE, using Matlab (The MathWorks™; www.mathworks.com/products/matlab/index.html.)
Chlorophyll-*a* concentration	CHL	mg/m^3	Monthly, 9 km resolution data from MODIS Aqua. (oceancolor.gsfc.nasa.gov/).
Surface temperature	SST	˚C	Monthly, 9 km resolution, 11µ nighttime data from MODIS Aqua. (oceancolor.gsfc.nasa.gov/).
Distance to a SST front	DIST_F	km	Calculated from SST, using the Cayula-Cornillon (1992) single-image detection algorithm, implemented in MGET (Roberts et al., 2010).

[1] Distance to the nearest pixel where ICE was greater than 0.

on three different occasions, the last transmission occurring 262 days after deployment, on 20 December (Fig. 2). From the first position on 30 April until 10 June, the whale moved back and forth in deep waters (> 1000 m) in the middle of the Fram Strait (between 77˚45′ N, 5˚ W and 80˚10′ N, 5˚ W) in an area known as the Northern Whaling Ground (Figs. 2 and 3). Then on 10 June it commenced a directed movement towards the southwest, staying in deep water close to the shelf. During the next 14 days, it traveled more than 950 km, ending up at 73˚40′ N, 15˚ W, where the movement pattern changed to a much less directed pattern (Figs. 2 and 3). That location is in the middle of an area known as the Southern Whaling Ground. The whale spent the period from 25 June to 17 July in the same area, still in deep water, before it swam onto the East Greenland shelf on 18 July at about 72˚20′ N, 18˚ W. The tag stopped sending signals for some months on 24 July (Figs. 2 and 3), when the whale was still in this general area. Then after about four months of silence, the tag transmitted several locations on 27 November (at 79˚56′ N, 04˚23′ E), on 13 December (at 80˚12′ N, 05˚09′ E), and again on 20 December (at 79˚10′ N, 02˚04′ E). These positions were only 61 km, 80 km, and 88 km away, respectively, from the position where the tag had been deployed 262 days earlier (Fig. 2).

The tracked bowhead whale spent most of its time in deep waters (87% of the time deeper than 1000 m; Fig. 3). Only in July, during the last week of the continuous tracking period, did it move onto the east Greenland shelf, where the depth is only about 250 m. During most of the tracking time, the whale was ice-associated, occupying relatively loose ice, mainly below 20% coverage. However, it did undertake several excursions out into open water (Fig. 3). These trips lasted for several days and took the whale up to 180 km away from the nearest ice edge.

FPTs at the chosen scale of 45 km ranged from 17 h to 299 h. When the whale stayed in the Northern and Southern Whaling Grounds, the FPTs were long (> 96 h; Fig. 2), except for the week-long excursion away from the ice during the first half of July (Figs. 2 and 3). During this excursion, and also during the directed movement between the Northern and Southern Whaling Grounds that took place from 10 June to 24 June, the FPTs were short—often shorter than 24 h (Fig. 2).

The rankings of all models used to fit FPTs as a function of environmental variables are presented in Table 2. There is no clear support for a single model ($w_i \geq 0.90$). Averaged coefficients for the 5 best models (bringing the $w_i \geq 0.90$) are thus shown in Table 3. Three environmental variables contributed significantly to the variability in habitat use intensities: distance to the ice (DIST_ICE), sea-ice concentrations (ICE), and sea bottom slope (SLO). The results of the models show that this bowhead whale usually remained in or close to ice-covered waters with modest ice concentrations, over areas where the bottom slope was relatively steep. More precisely, the probabilities of leaving an area increased with distance to the sea ice (DIST_ICE), by 12% per 10 km; increased with sea-ice concentration (ICE), by 62% per 10% ice concentration; and decreased with increasing sea-bottom slope (SLO), by 75% per 10% increase in slope.

DISCUSSION

Whaling that targeted bowhead whales from the Spitsbergen stock commenced in 1611, concentrating first on the huge numbers of whales found in the fiords and close to the shores of Svalbard, mainly on the west coast of Spitsbergen, the biggest island of the archipelago (Ross, 1993). After some few decades of intense whaling, this so-called "bay whaling" was abandoned because of the scarcity of whales, and a pelagic whaling period was initiated. During this period, which lasted until whaling more or less ceased in the late 1800s, the whaling vessels cruised along the pack-ice edges between Spitsbergen and Greenland. It was in this area that the whale in this study was tracked. Many of the recent observations of bowhead whales were also made there (Wiig et al., 2010a) even though in comparison to the coastal areas of Svalbard, few ships traverse the zone. The bowhead whales hunted during the early bay whaling period were probably extirpated, while some few of the offshore bowhead whales survived the commercial whaling period thanks to the vastness of this area and the protection afforded by the drifting ice. Data from three dedicated visual and acoustic surveys during the last five years (Wiig et al., 2007, 2008, 2010a, b) suggest that the

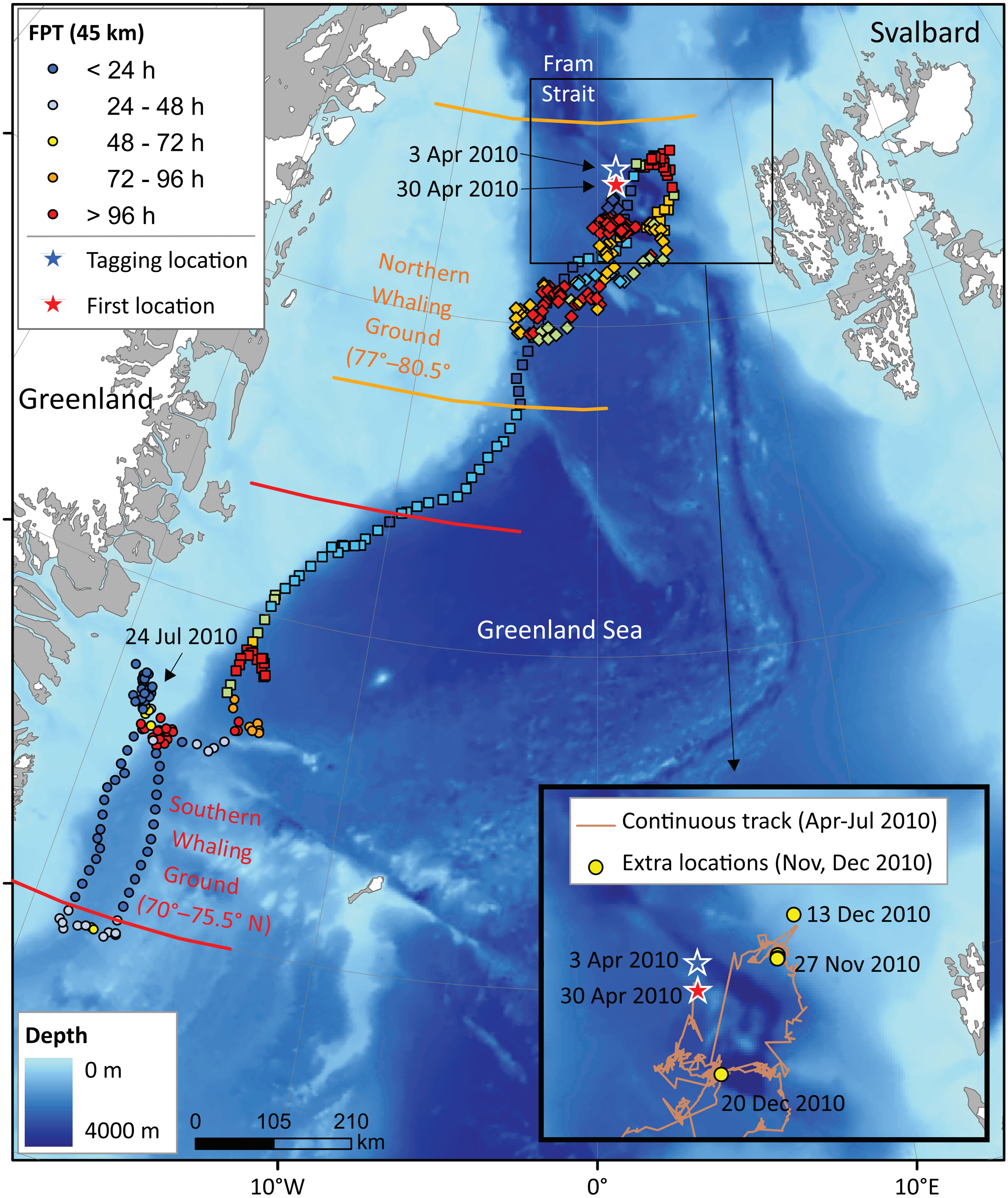

FIG. 2. Track of a bowhead whale equipped with a satellite tag. Star indicates tagging location. Colours as shown in legend indicate first-passage time (FPT, 45 km radius); ◊ represents positions in May, □ represents positions in June, and ○ represents positions in July. The whale was tagged on 3 April 2010 and sent locations continuously from 30 April to 24 July 2010. Additional locations obtained in November and December 2010 are presented in the inset.

number of whales occurring along this ice edge is still likely to be very low. However, there is some indication of a possible increase in the number of animals along the east coast of Greenland (Gilg and Born, 2005; Boertmann et al., 2009; Boertmann and Nielsen, 2010). Additionally, some animals occupy areas deep within the pack ice,

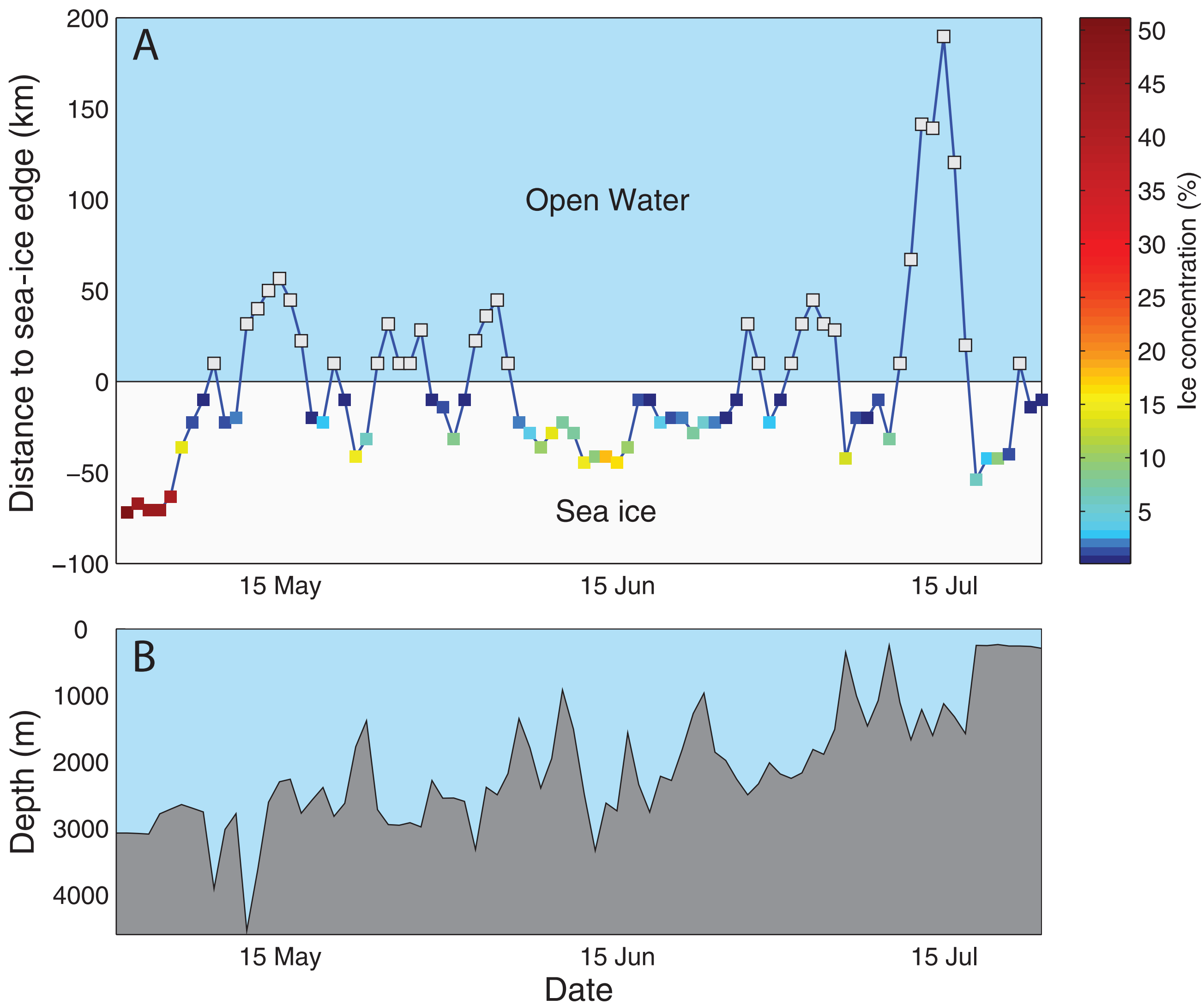

FIG. 3. (A) Distance of the whale from the sea-ice edge daily at 12:00 and sea-ice concentration at the location of the whale (open-water locations are shown in grey). (B) Water depth in which the bowhead traveled.

which are inaccessible to standard survey ships (Stafford et al., 2010).

The tag that was deployed on the bowhead whale in the present study must have been attached to the animal for at least 262 days. The reason for the initial delay in sending signals is assumed to be related to the way the tag is constructed and the pressure with which it was deployed. The tag consists of a 21 cm long anchor-shaft (7 mm diameter) with a sharp triangular tip and a thicker cylindrical transmitter section (2 cm diameter, 8 cm long), all of stainless steel, and all of which should enter the blubber of the whale. Deeper penetration is prevented by a stopping plate (diameter 3.7 cm) that separates the external part of the tag from the part that is supposed to be in the blubber. The outer part of the tag consists of the remaining part of the transmitter cylinder (2 cm diameter, 3.7 cm long), which has both an antenna and a saltwater switch. During deployment, we came unexpectedly close to the whale, and the 12 bar pressure used to deploy the tag likely forced the stopping plate through the skin into the blubber. When we resighted the whale 10 days after the tag deployment, we could see the antennae, so the tag could not have penetrated much deeper than intended. But the steel cylinder is one of the terminals for the saltwater switch, and if the entire cylinder were embedded in blubber, the tag would not begin to transmit until some of this part of the tag made contact with saltwater. We think that the embedded tag gradually grew out of the blubber as part of a natural rejection/healing process and was eventually exposed to saltwater, allowing the tag to start up. When transmissions ceased after about three months, we assumed that the tag had fallen off the whale. This was obviously wrong, since we received locations on three different occasions some months later, up to 262 days post-deployment. All of these small clusters of locations were credible location data. We have no explanation for the erratic tag performance; clearly the tag was still attached to

TABLE 2. Model selection based on the Akaike's information criteria corrected to the actual sample size (AIC_c) and Akaike weights (w_i). The best set of models ($w > 0.9$) is presented in bold. AIC_c differences (Δ_i) are also presented, together with the sample size (n), log-likelihoods (log(L)), and degrees of freedom (df) used to calculate the AIC_c values. See Table 1 for definition of the variable abbreviations.

	Model	AIC_c	Δ_i	w_i	n	log(L)	df
1	**CHL + SST + DIST_ICE + ICE + SLO**	**764.3**	0	**0.44**	106	-377	5
2	**CHL + SST + DIST_ICE + ICE + SLO + DEP**	**766.0**	1.7	**0.19**	106	-377	6
3	**CHL + SST + DIST_ICE + ICE + SLO + DIST_F**	**766.6**	2.2	**0.14**	106	-377	6
4	**CHL + SST + DIST_ICE + ICE**	**767.7**	3.3	**0.08**	106	-380	4
5	**CHL + SST + DIST_ICE + ICE + SLO + DEP + DIST_F**	**768.3**	4.0	**0.06**	106	-377	7
6	CHL + SST + DIST_ICE + ICE + DIST_F	769.8	5.4	0.03	106	-380	5
7	CHL + SST + DIST_ICE + SLO	769.8	5.5	0.03	106	-381	4
8	CHL + SST + DIST_ICE + ICE + DEP	769.9	5.5	0.03	106	-380	5
9	CHL + SST + DIST_ICE	774.3	9.9	0.00	106	-384	3
10	CHL + SST + DIST_ICE + DEP	775.1	10.8	0.00	106	-383	4
11	CHL + SST + DIST_ICE + DIST_F	776.4	12.1	0.00	106	-384	4
12	CHL + SST + SLO	780.2	15.8	0.00	106	-387	3
13	CHL + SST + ICE	782.5	18.1	0.00	106	-388	3
14	CHL + SST + DIST_F	783.0	18.6	0.00	106	-388	3
15	CHL + SST	784.5	20.2	0.00	106	-390	2
16	CHL + SST + DEP	786.3	21.9	0.00	106	-390	3
17	CHL + DIST_ICE	790.8	26.4	0.00	108	-393	2
18	CHL + SLO	797.6	33.3	0.00	108	-397	2
19	CHL + DIST_F	799.8	35.4	0.00	108	-398	2
20	CHL + ICE	801.7	37.3	0.00	108	-399	2
21	CHL	803.1	38.8	0.00	108	-401	1
22	CHL + DEP	803.4	39.1	0.00	108	-400	2
23	SST	1067.0	302.6	0.00	138	-532	1
24	DIST_ICE	1088.5	324.2	0.00	140	-543	1
25	DEP	1096.8	332.5	0.00	140	-547	1
26	DIST_F	1103.8	339.4	0.00	140	-551	1
27	SLO	1104.6	340.3	0.00	140	-551	1
28	ICE	1108.8	344.4	0.00	140	-553	1

TABLE 3. Summary of parameter estimates (β) for the covariates included in the best set of models used to fit habitat-use intensities (first-passage times at a 45 km scale) as a function of environmental variables. Range of observed values, averaged coefficients, their 95% confidence intervals (CI), and hazard ratios [exp(β)] are shown for each covariate. A β coefficient equal to zero (whose CI includes 0) indicates no effect of the covariate (non-bold text). Bold text shows effects: a positive β (with corresponding hazard ratio higher than one) indicates an increased probability of leaving, and a negative β (hazard ratio lower than one), a decreased probability. See Table 1 for definition of the variable abbreviations.

Covariate	DEP	SLO	ICE	DIST_ICE	CHL	SST	DIST_F
Range	244–4241 m	0.1–27.0%	0–57%	0–190 km	0.1–3.4 mg/m³	-1.9–3.3ºC	0–87 km
β: (model 1)		-0.076	0.058	0.011	0.159	-0.006	
(model 2)	0.000	-0.083	0.063	0.011	0.153	0.037	
(model 3)		-0.077	0.058	0.012	0.153	-0.004	-0.001
(model 4)			0.062	0.012	0.250	0.037	
(model 5)	0.000	-0.084	0.062	0.012	0.150	0.038	-0.001
Average (β)	0.000	**-0.078**	**0.060**	**0.011**	0.165	0.010	-0.001
CI	0.000	**-0.150**	**0.020**	**0.010**	-0.240	-0.170	-0.010
	0.000	**-0.010**	**0.100**	**0.020**	0.570	0.190	0.010
exp (β)	1.000	**0.925**	**1.062**	**1.012**	1.179	1.010	0.999

the whale, so it must have experienced technical failure of some type.

During the periods of directed movements between the Northern and Southern Whaling Grounds, this bowhead whale covered a straight-line distance of 950 km, corresponding to a daily movement rate of about 70 km per day. This rate is considerably higher than what was reported for 27 bowhead whales tagged in Foxe Basin and Cumberland Sound (Ferguson et al., 2010a), but slower than speeds reported for bowhead whales crossing from West Greenland to Canada, for which daily distances of over 100 km were reported (Heide-Jørgensen et al., 2003). The directionality of this movement from north towards south during summer is quite unusual for a bowhead whale; in fact, it is opposite to the normal seasonal movement patterns described for other bowhead whale stocks, which move north during summer and then south again before the winter (Heide-Jørgensen et al., 2006; Quakenbush et al., 2010). We must, of course, bear in mind that this study is based on data from only a single individual, but the movement pattern undertaken by this individual is in remarkable accordance with what was common knowledge to the early whalers and later

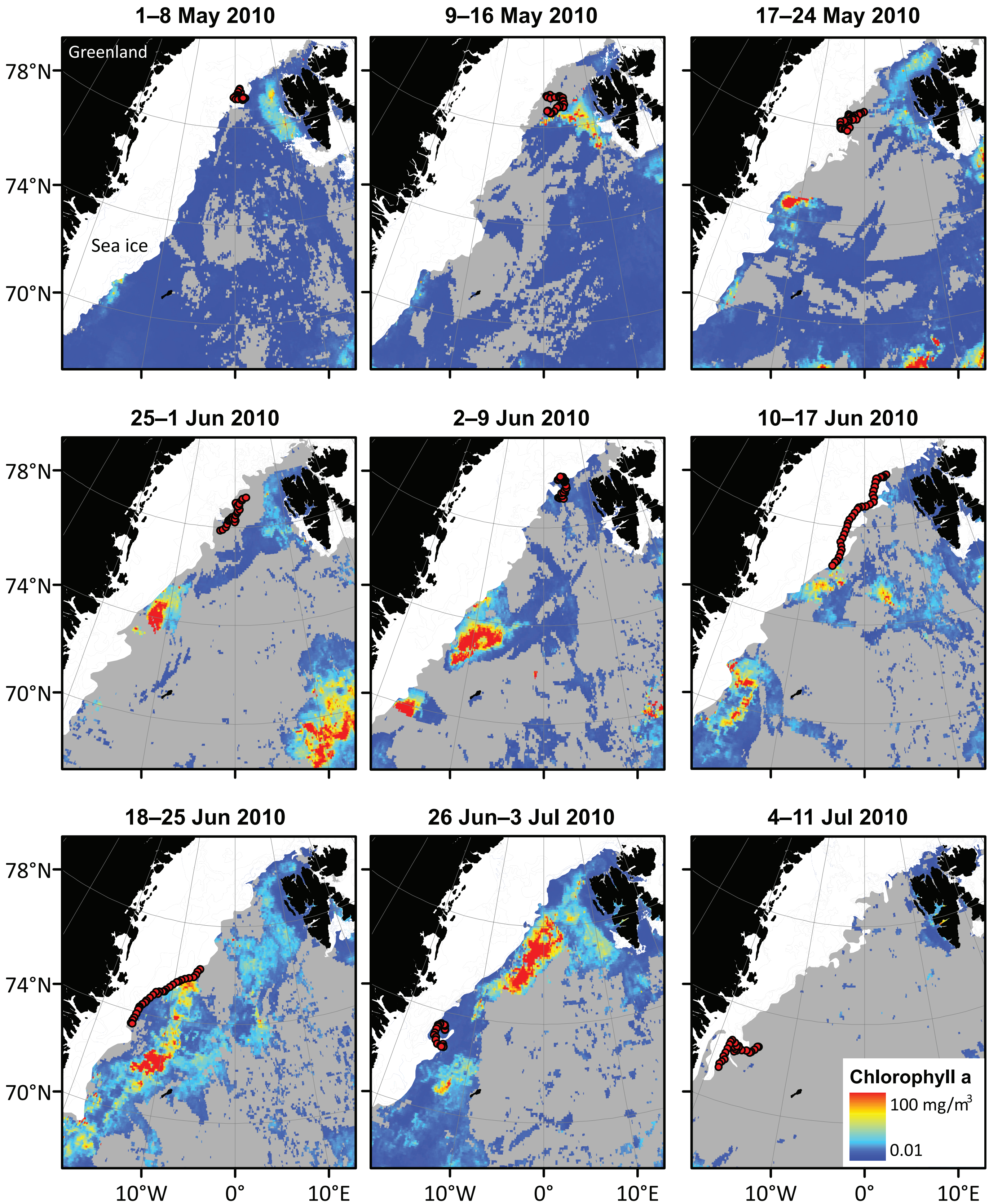

FIG. 4. Weekly locations of a bowhead whale (red circles) and chlorophyll-*a* concentrations (9 km Modis-Aqua data; the colour bar is in a logarithmic scale). Sea-ice coverage (10%–100% concentration) for day number four of each week is shown in white (data provided by the Norwegian Meteorological Institute). Areas with no chlorophyll-*a* data (because clouds were present) are illustrated in grey.

reported in the late 19th and early 20th centuries (Southwell, 1898; Gray, 1931). The whalers described starting the season in April-May in the Northern Whaling Grounds at about 80˚ N, or as far north as one could get, depending on the ice in a given year (Southwell, 1898; Gray, 1931). By the middle or end of June, the whales moved south on a path more or less parallel with the Greenland coast, depending on the ice extent, and were again targeted on the Southern Whaling Grounds in July and August (Southwell, 1898; Gray, 1931). The tagged whale in our study is thus doing exactly what was described in these old publications. These whale movements, according to Gray (1931), were related to food distribution. He describes how the whalers searched for areas where the ocean was an opaque green. This coloration was caused by diatom blooms, which attract the copepods upon which bowhead whales feed (Gray, 1931). Gray (1931) further suggested that the green-coloured water masses drifted south and west with the currents and the bowhead whales followed them. Phytoplankton blooms in the Arctic normally follow the northward receding ice edge as it successively exposes new water masses to light (Sakshaug and Skjoldal, 1989). But the existence of an algae bloom up north in the Northern Whaling Ground in May that drifts south and west with the current, as suggested by Gray (1931), was confirmed by remote sensing in 2010 (Fig. 4). Recent studies also confirm that the spring phytoplankton bloom in this area still consists mainly of diatoms (Rey et al., 2000). However, our whale's movements were not directly correlated to chlorophyll concentrations, although the whale moved in the same general direction as the bloom (Fig. 4).

Our tracked whale seemed to prefer waters with relatively loose ice cover in areas where the bottom slope was relatively steep (Table 3). The affiliation between bowhead whales and sea ice has recently been explored in the Eastern Canada – West Greenland stock (Ferguson et al., 2010a). On the basis of data from 27 individuals, Ferguson et al. (2010a) suggested that in summer, the whales preferred high ice concentrations (> 65%) with thick first-year ice and open water and that they avoided areas with large ice floes (> 2 km). Selection of this specific type of ice was considered to be related to avoidance of killer whale predation. Killer whales are predators of bowhead whales (Ford and Reeves, 2008; Ferguson et al., 2010b), but killer whales tend to stay away from areas with high ice concentrations (Matthews et al., 2011), probably to avoid damage to their large dorsal fin. In recent years, poor ice conditions in the eastern Canadian Archipelago have allowed this predator to travel farther into the Arctic, and in Foxe Basin, bowhead whales from the Eastern Canada – West Greenland stock have apparently been exposed to a dramatic increase in predation from killer whales (Ferguson et al., 2010b). However, the whale in our study was never associated with ice concentration above 65%. In addition, it also undertook several long trips out into open water, trips that lasted up to a week and distanced the whale up to 180 km from the ice edge (Figs. 2 and 3). Killer whales were observed on several occasions during the various bowhead whale surveys in the Greenland Sea, and a group of at least three individuals visited our research vessel at 79˚54′ N and 2˚13′ E a few hours before the bowhead whale in this study was tagged. During our bowhead whale survey in 2008, we observed killer whales (6 – 8 individuals) as far north as 80˚10′ N (at 3˚41′ E) as early as 11 March. These are likely all mammal-eating killer whales since there are no known fish resources suitable for killer whales in this area at this time of year. We never detected killer whale sounds during any of the three bowhead whale surveys (Wiig et al., 2007, 2008, 2010a, b), a pattern which is in accordance with the acoustic behaviour of mammal-eating killer whales from other areas (e.g., Barrett-Lennard et al., 1996). Nor did we ever detect bowhead whales acoustically during any of the survey efforts, which might, in turn, be related to the presence of killer whales. The fact that the whale preferred to stay over areas with steeply sloping bottom topography (Table 3) could be related to bathymetrically steered upwelling, which makes such areas productive (Miller, 2003). However, the ice edge in the area is basically co-incident with the continental slope (see Figs. 2 and 4), so we cannot separate the potential influence of the slope from affiliation with the ice alone. It should also be noted in this context that bowhead whales have been observed along the coast of East Greenland in shallow shelf waters (Gilg and Born, 2005; Boertmann et al., 2009).

The locations from November and December show that the whale returned to 80˚ N, suggesting that the overwintering site for this individual is at this latitude. This conclusion is the only result from our study that is not in accordance with the old historical literature, which suggested that the bowhead whales overwintered in the southwest Greenland Sea near Iceland (Southwell, 1898). One cannot make firm conclusions on the basis of tracking data from one animal, but information from a recently deployed AURAL (Autonomous Underwater Recorder for Acoustic Listening) at 78˚49′ N and 4˚59′ W confirms that bowhead whales do overwinter near the Northern Whaling Ground (Stafford et al., 2010). During the historical whaling period, no ships would have been able to search for whales in these northerly areas during winter because of weather, ice, and light conditions (total darkness). It could therefore be that the early whalers were simply guessing where the bowhead whales overwintered on the basis of general observations in the fall (Southwell, 1898), or that a fraction of the Spitsbergen stock, which may or may not be there today, did overwinter near Iceland.

In this study, we have presented tracking data from a female bowhead whale from the Spitsbergen stock. After spending some weeks in the Northern Whaling Ground at about 78˚ – 80˚ N, this single animal moved quickly in a southwestern direction down to the Southern Whaling Grounds at about 70˚ – 73˚ N. The directionality of this summer movement is opposite to the general movement patterns for bowhead whales from other stocks, but in close agreement with historical records about movements of whales in the Spitsbergen stock collected hundreds of years ago. The crustaceans that the whales feed on drift with the strong southward current along the ice edge from the northeast toward the southwest parts of the Greenland Sea over the summer; the large outflow of Arctic water in the Fram Strait area and concomitant ecological impacts are the likely reason for the atypical movement patterns of bowhead whales in this area. Data from the tracked individual, supported by data from acoustic listening devices, suggest that the Spitsbergen bowhead stock overwinters near the Northern Whaling Ground.

ACKNOWLEDGEMENTS

We thank Eirik Grønningsæter, Tonje K. Sørdalen, Jørgen R. Wiig, and the crew on RV *Lance* for help in the field and Mikkel Willum for use of equipment. This study was financed by the Norwegian Polar Institute, with additional support from the Natural History Museum, University of Oslo, and the Greenland Institute of Natural Resources. This study was done under permit of the Norwegian Animal Research Authority.

REFERENCES

Allen, R.C., and Keay, I. 2006. Bowhead whales in the eastern Arctic, 1611–1911: Population reconstruction with historical whaling records. Environment and History 12:89–113.

Barrett-Lennard, L.G., Ford, J.K.B., and Heise, K.A. 1996. The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. Animal Behaviour 51:553–565.

Boertmann, D., and Nielsen, R.D. 2010. A bowhead whale calf observed in northeast Greenland waters. Polar Record 46:373–375.

Boertmann, D., Merkel, F., and Durinck, J. 2009. Bowhead whales in East Greenland, summers 2006-2008. Polar Biology 32:1805–1809.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. New York: Springer-Verlag.

Cayula, J.-F., and Cornillon, P. 1992. Edge detection algorithm for SST images. Journal of Atmospheric and Oceanic Technology 9:67–80.

Fauchald, P., and Tveraa, T. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. Ecology 84:282–288.

Ferguson, S.H., Dueck, L., Loseto, L.L., and Luque, S.P. 2010a. Bowhead whale *Balaena mysticetus* seasonal selection of sea ice. Marine Ecology Progress Series 411:285–297.

Ferguson, S.H., Higdon, J.W., and Chmelnitsky, E.G. 2010b. The rise of killer whales as a major Arctic predator. In: Ferguson, S.H., Loseto, L.L., and Mallory, M.L., eds. A little less Arctic: Top predators in the world's largest northern inland sea, Hudson Bay. New York: Springer Publishing Co. 117–136.

Ford, J.K.B., and Reeves, R.R. 2008. Fight or flight: Antipredator strategies of baleen whales. Mammal Review 38:50–86.

Freitas, C., Lydersen, C., Fedak, M.A., and Kovacs, K.M. 2008a. A simple new algorithm to filter marine mammal Argos locations. Marine Mammal Science 24:315–325.

Freitas, C., Kovacs, K.M., Lydersen, C., and Ims, R.A. 2008b. A novel method for quantifying habitat selection and predicting habitat use. Journal of Applied Ecology 45:1213–1220.

George, J.C., Zeh, J., Suydam, R., and Clark, C. 2004. Abundance and population trend (1978–2001) of Western Arctic bowhead whales surveyed near Barrow, Alaska. Marine Mammal Science 20:755–773.

Gerber, L.R., Keller, A.C., and DeMaster, D.P. 2007. Ten thousand and increasing: Is the Western Arctic population of bowhead whale endangered? Biological Conservation 137:577–583.

Gilg, O., and Born, E.W. 2005. Recent sightings of the bowhead whale (*Balaena mysticetus*) in Northeast Greenland and the Greenland Sea. Polar Biology 28:796–801.

Givens, G.H., Huebinger, R.M., Patton, J.C., Postma, L.D., Lindsay, M., Suydam, R.S., George, J.C., Matson, C.W., and Bickham, J.W. 2010. Population genetics of bowhead whales (*Balaena mysticetus*) in the Western Arctic. Arctic 63:1–12.

Gray, R.W. 1931. The colour of the Greenland Sea and the migration of the Greenland whale and narwhal. Geographical Journal 78:284–290.

Heide-Jørgensen, M.P., Kleivane, L., Øien, N., Laidre, K.L., and Jensen, M.V. 2001. A new technique for deploying satellite transmitters on baleen whales: Tracking a blue whale (*Balaenoptera musculus*) in the North Atlantic. Marine Mammal Science 17:949–954.

Heide-Jørgensen, M.P., Laidre, K.L., Wiig, Ø., Jensen, M.V., Dueck, L., Maiers, L.D., Schmidt, H.C., and Hobbs, R.C. 2003. From Greenland to Canada in ten days: Tracks of bowhead whales, *Balaena mysticetus*, across Baffin Bay. Arctic 56:21–31.

Heide-Jørgensen, M.P., Laidre, K.L., Jensen, M.V., Dueck, L., and Postma, L.D. 2006. Dissolving stock discreteness with satellite tracking: Bowhead whales in Baffin Bay. Marine Mammal Science 22:34–45.

Heide-Jørgensen, M.P., Laidre, K.L., Wiig, Ø., Postma, L., Dueck, L., and Bachmann, L. 2010. Large-scale sexual segregation of bowhead whales. Endangered Species Research 13:73–78.

IWC (International Whaling Commission). 2010. Report of the Scientific Committee. Journal of Cetacean Research and Management 11 (Suppl. 2). 627 p.

Jakobsson, M., Macnab, R., Mayer, L., Anderson, R., Edwards, M., Hatzky, J., Schenke, H.W., and Johnson, P. 2008. An improved bathymetric portrayal of the Arctic Ocean: Implications for ocean modeling and geological, geophysical and oceanographic analyses. Geophysical Research Letters 35, L07602, doi:10.1029/2008GL033520.

Johnson, J.B., and Omland, K.S. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19:101–108.

Krutzikowsky, G.K., and Mate, B.R. 2000. Dive and surfacing characteristics of bowhead whales (*Balaena mysticetus*) in the Beaufort and Chukchi seas. Canadian Journal of Zoology 78:1182–1198.

Laidre, K.L., Heide-Jørgensen, M.P., and Nielsen, T.G. 2007. Role of the bowhead whale as a predator in West Greenland. Marine Ecology Progress Series 346:285 – 297.

Laidre, K.L., Heide-Jørgensen, M.P., Logsdon, M.L., Delwiche, L., and Nielsen, T.G. 2010. A whale of an opportunity: Examining the vertical structure of chlorophyll-*a* in high Arctic waters using instrumented marine predators. Marine Biology Research 6:519 – 529.

Mate, B.R., Krutzikowsky, G.K., and Winsor, M.H. 2000. Satellite-monitored movements of radio-tagged bowhead whales in the Beaufort and Chukchi seas during the late-summer feeding season and fall migration. Canadian Journal of Zoology 78:1168 – 1181.

Matthews, C.J.D., Luque, S.P., Petersen, S.D., Andrews, R.D., and Ferguson, S.H. 2011. Satellite tracking of a killer whale (*Orcinus orca*) in the eastern Canadian Arctic documents ice avoidance and rapid, long-distance movement into the North Atlantic. Polar Biology 34:1091 – 1096.

Miller, C.B. 2003. Biological oceanography. Malden, Massachusetts: Blackwell.

Palsbøll, P.J., Larsen, F., and Hansen, E.S. 1991. Sampling of skin biopsies from free-ranging large cetaceans in West Greenland: Development of new biopsy tips and bolt design. Report of the International Whaling Commission Special Issue 13:71 – 79.

Palsbøll, P.J., Vader, A., Bakke, I., and El-Gewely, M.R. 1992. Determination of gender in cetaceans by the polymerase chain-reaction. Canadian Journal of Zoology 70:2166 – 2170.

Quakenbush, L.T., Citta, J.J., George, J.C., Small, R.J., and Heide-Jørgensen, M.P. 2010. Fall and winter movements of bowhead whales (*Balaena mysticetus*) in the Chukchi Sea and within a potential petroleum development area. Arctic 63:289 – 307.

R Development Core Team. 2010. The R Project for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. www.r-project.org.

Reilly, S.B., Bannister, J.L., Best, P.B., Brown, M., Brownell, R.L., Jr., Butterworth, D.S., Clapham, P.J., et al. 2008. *Balaena mysticetus* (Svalbard-Barents Sea (Spitsbergen) subpopulation). In: The IUCN Red List of Threatened Species. www.iucnredlist.org.

Rey, F., Noji, T.T., and Miller, L.A. 2000. Seasonal phytoplankton development and new production in the central Greenland Sea. Sarsia 85:329 – 344.

Roberts, J.J., Best, B.D., Dunn, D.C., Treml, E.A., and Halpin, P.N. 2010. Marine geospatial ecology tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. Environmental Modelling and Software 25:1197 – 1207.

Ross, W.G. 1993. Commercial whaling in the North Atlantic sector. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. Society for Marine Mammalogy, Special Publication No. 2. Lawrence, Kansas: Allen Press. 511 – 561.

Sakshaug, E., and Skjoldal, H.R. 1989. Life at the ice edge. Ambio 18:60 – 67.

Stafford, K.M., Moore, S.E., Berchok, C., Melling, H., Wiig, Ø., Kovacs, K.M., and Lydersen, C. 2010. Passive acoustic monitoring for marine mammals at two sites in the Arctic Ocean: The Chukchi Plateau and Fram Strait (Abstract only). Proceedings from the International Polar Year Conference, 8 – 12 June 2010, Oslo, Norway.

Southwell, T. 1898. The migration of the right whale (*Balaena mysticetus*). Natural Science 12:397 – 414.

Wiig, Ø., Bachmann, L., Janik, V.M., Kovacs, K.M., and Lydersen, C. 2007. Spitsbergen bowhead whales revisited. Marine Mammal Science 23:688 – 693.

Wiig, Ø., Bachmann, L., Berge, J., Janik, V.M., Kovacs, K.M., Swift, R., and Lydersen, C. 2008. Surveys of bowhead whales (*Balaena mysticetus*) in the Northeast Atlantic in 2006 and 2008. International Whaling Commission SC/60/BRG32. 5 p.

Wiig, Ø., Bachmann, L., Øien, N., Kovacs, K.M., and Lydersen, C. 2010a. Observations of bowhead whales (*Balaena mysticetus*) in the Svalbard area 1940 – 2009. Polar Biology 33:979 – 984.

Wiig, Ø., Bachmann, L., Kovacs, K.M., Swift, R., and Lydersen, C. 2010b. Survey of bowhead whales (*Balaena mysticetus*) in the Northeast Atlantic in 2010. International Whaling Commission SC/62/BRG20. 2 p.

Woodby, D.A., and Botkin, D.B. 1993. Stock sizes prior to commercial whaling. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. Society for Marine Mammalogy, Special Publication No. 2. Lawrence, Kansas: Allen Press. 387 – 407.

Zeh, J.E., Clark, C.W., George, J.C., Withrow, D., Carroll, G.M., and Koski, W.R. 1993. Current population size and dynamics. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. Society for Marine Mammalogy, Special Publication No. 2. Lawrence, Kansas: Allen Press. 409 – 489.