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Identification of Potential Foraging Areas for Bowhead Whales in Baffin Bay and Adjacent Waters

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ABSTRACT. The bowhead whale (*Balaena mysticetus*) is the Arctic's largest and most dependent predator on zooplankton; however, knowledge about its important foraging areas in Baffin Bay and adjacent waters is limited. Data on movement, horizontal velocity (ms^{-1}), dive depth (m), and dive rate (dives h^{-1}) were obtained from 39 bowhead whales (31 females, 6 males, and 2 of undetermined sex) instrumented with satellite-linked time-depth recorders (SLTDRs) in spring 2009 and 2010 in Disko Bay, West Greenland. Thirty-eight whales provided information on dive rates and movement, and potential foraging areas were identified on the basis of low dive rates and stationary behaviour. Nine potential foraging areas were identified: Disko Bay and adjacent region, Clyde Inlet, Isabella Bay, Broughton Island, Cumberland Sound, Frobisher Bay, Hudson Strait, southern Foxe Basin, and northern Foxe Basin. Two females returned to Disko Bay the following spring (duration of tags > 420 days). Their diving behavior indicated that all whales exhibited a large degree of flexibility in their use of potential feeding areas in Baffin Bay and adjacent waters. The variability of habitat selection may buffer against climate-induced changes in the preferred habitats of bowhead whales.

Key words: foraging; bowhead whale; *Balaena mysticetus*; satellite telemetry; SLTDR; Baffin Bay; climate change

RÉSUMÉ. La baleine boréale (*Balaena mysticetus*) est le plus grand prédateur de zooplancton de l'Arctique. Elle est également le prédateur qui dépend le plus de cette espèce. Cependant, on possède peu de connaissances sur les importantes zones d'alimentation de la baleine boréale dans la baie de Baffin et les eaux adjacentes. Des données au sujet des déplacements et de la vélocité horizontale (ms^{-1}), de la profondeur des plongeons (m) et du taux de plongeons (plongeons h^{-1}) ont été obtenues à partir de 39 baleines boréales (31 femelles, six mâles et deux baleines au sexe non déterminé) dotées d'enregistreurs de profondeur temporelle satellitaires (SLTDR) au printemps 2009 et au printemps 2010 dans la baie de Disko, dans l'ouest du Groenland. Trente-huit baleines ont permis d'obtenir de l'information sur le taux de plongeons et les déplacements, de même que sur les zones d'alimentation potentielles en fonction des plongeons en faible profondeur et du comportement stationnaire. Neuf zones d'alimentation potentielles ont été déterminées, soit la baie de Disko et la région adjacente, le passage Clyde, la baie Isabella, la baie Broughton, le détroit de Cumberland, la baie Frobisher, le détroit d'Hudson, le sud du bassin Foxe et le nord du bassin Foxe. Deux femelles sont retournées à la baie de Disko le printemps suivant (durée des étiquettes > 420 jours). Leur comportement de plongée laissait entrevoir que toutes les baleines possédaient un grand degré de souplesse quant à leur utilisation des zones d'alimentation potentielles dans la baie de Baffin et les eaux adjacentes. La variabilité de la sélection de l'habitat peut avoir pour effet d'amortir les changements découlant du climat dans les habitats préférés des baleines boréales.

Mots clés : alimentation; baleine boréale; *Balaena mysticetus*; télémesure satellitaire; SLTDR; baie de Baffin; changement climatique

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INTRODUCTION

The rise in global temperature is forecast to continue and will be amplified in polar regions (Serreze et al., 2009; Screen and Simmonds, 2010). The top marine predators in the Arctic are likely to respond to these changes and may have different strategies for adaptations in this environment. However, top predators are particularly challenging to study because their spatial ranges are large and their habitats are not clearly delineated (Laidre et al., 2008; Moore and Huntington, 2008). The bowhead whale (*Balaena mysticetus*) is endemic to the Arctic, and it is the largest and most dependent predator of zooplankton. Information on the prey and key foraging areas of bowheads in Baffin Bay and adjacent waters is limited, and detailed information on their dive behaviour has been obtained only for Disko Bay, West Greenland (Heide-Jørgensen et al., 2006, 2012a, 2013; Pomerleau et al., 2011a).

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Studies of bowhead whale stomachs sampled in April and May from Disko Bay demonstrated that these whales have a strong preference for calanoid copepods (Heide-Jørgensen et al., 2012b), a resource that is known to be abundant in Disko Bay (Madsen et al., 2001). As the sea ice is breaking up in spring, copepods ascend towards the surface to graze on primary producers in the upper 100 m; thus, they are closely coupled with phytoplankton production (Madsen et al., 2001; Laidre et al., 2007; Heide-Jørgensen et al., 2013). Analysis of stomach contents from harvested bowhead whales outside Baffin Bay indicates that they have a more varied diet than *Calanus* spp. In the Canadian Arctic Archipelago and the Alaskan Beaufort Sea, they also feed on amphipods such as hyperiids, euphausiids, and mysids (Carroll et al., 1987; Lowry et al., 2004; Pomerleau et al., 2011b). However, a recent study of stable isotopes in bowhead whales confirmed that they also rely heavily on copepods in areas outside Disko Bay (Pomerleau et al., 2012).

Bowhead whales arrive in Disko Bay, their most important feeding ground in West Greenland, around January and February (Laidre et al., 2008; Laidre and Heide-Jørgensen, 2012; Heide-Jørgensen et al., 2013; Rekdal et al., 2015). Satellite tracking studies of bowheads in West Greenland have shown that they depart Disko Bay in mid to late May and move almost diagonally northwest, crossing Baffin Bay and reaching Bylot Island between late May and July (Heide-Jørgensen et al., 2003a, 2012b; Laidre and Heide-Jørgensen, 2012). This route has also been described by Inuit hunters and commercial whalers since the 19th century (Southwell, 1898); however, those observers also located bowhead whales farther north along the west coast of Greenland before the whales crossed Baffin Bay. In fall, bowhead whales move south along eastern Baffin Island, and in late November they enter Hudson Strait, which is believed to be one of their main wintering grounds (Heide-Jørgensen et al., 2006; Koski et al., 2006). Previous studies of bowhead whales in the eastern Canadian Arctic used satellite telemetry and observational data to identify important areas (Finley, 1990; Pomerleau et al., 2011b; Wheeler et al., 2012); however, no study has used data on diving patterns from whales tagged in Disko Bay to identify foraging areas outside of West Greenland.

Knowledge of foraging behaviour is scarce; however, it has been suggested that bowhead whales make long-duration foraging dives, which result in a small number of dives per hour (Laidre et al., 2007; Heide-Jørgensen et al., 2013). The foraging dive is characterized by a U-shape: the whale descends to a specific depth, opens its mouth while moving slowly and horizontally for an average of ca. 15 min, and then ascends to the surface again (Heide-Jørgensen et al., 2013). Bowhead whales often target a certain depth during a series of foraging dives (Laidre et al., 2007). The depth of a U-shaped foraging dive appears to depend on zooplankton distribution, and therefore target depth varies with time of year and location.

In this study we identified potential feeding areas of the Eastern Canada–Western Greenland (EC-WG) stock of bowhead whales using movement and dive data collected from satellite transmitters. We instrumented 44 bowhead whales with satellite transmitters, and 39 transmitters relayed daily locations and summarized (binned) dive depth data. These data provide insight into the ecology and adaptability of bowhead whales as well as informing conservation and management decisions.

MATERIAL AND METHODS

Instrumentation of Bowhead Whales

Adult bowhead whales (> 13 m in length, George et al., 2004) were instrumented with satellite-linked time-depth recorders (SLTDRs) during March–May in 2009 and 2010 from Qeqertarsuaq (Disko Island, West Greenland, Fig. 1). The transmitters were manufactured by Wildlife Computers (Redmond, Washington, USA) and modified for use on whales by M.V. Jensen (www.mikkelvillum.com). Data were relayed through the Argos Data Collection and Location System and decoded using Argos Message Decoder (DAP Ver. 3.0, build 114, Wildlife Computers). Two types of tags were used, both of which were designed to be implanted in the blubber and muscle of the whales. The internally positioned MK10 tag consisted of a 151 × 22 mm stainless steel tube, with a stop plate (38 mm in diameter) that prevented the tag from being implanted deeper than 113 mm. The tag was anchored with a 205 × 8 mm cylindrical stainless steel anchoring spear (tulip anchor) equipped with a sharp-pointed triangular tip and foldable barbs (40–50 mm) along the spear to impede expulsion from the blubber-muscle layer. The rear end of the steel tube had a 160 mm antenna and a saltwater switch to ensure that transmissions occurred only when the rear part of the tag was out of the water. The pressure transducer was positioned just below the stop plate. The weight of the transmitter with the anchoring spear was 250 g, and the tag had one AA cell in the front part of the steel tube. The externally positioned tag (SPLASH) used an anchoring spear similar to that used for the MK10 to anchor the tag, but the transmitter was mounted on a steel plate attached to the rear end of the anchoring spear and sat externally on the whale. The anchoring spear was 235 × 8 mm, of which 210 mm was implanted into the blubber and muscle layer with barbs, and 25 mm remained outside the skin. The steel plate with the transmitter (85 × 50 × 25 mm) could swivel freely around the spear to keep the tag in a position with the least drag in the water. A saltwater switch and pressure transducer were mounted on top of the transmitter next to the antenna and the tag. Total weight of the SPLASH tag was 300 g, with two AA cells as power supply.

Daily searches for whales were conducted in the northern part of Disko Bay on days with good visibility and low sea state (Beaufort sea state 0 or 1) from two to four small (6 m) boats with outboard engines (150 hp). As soon as a whale was spotted, the boats quickly moved close to the

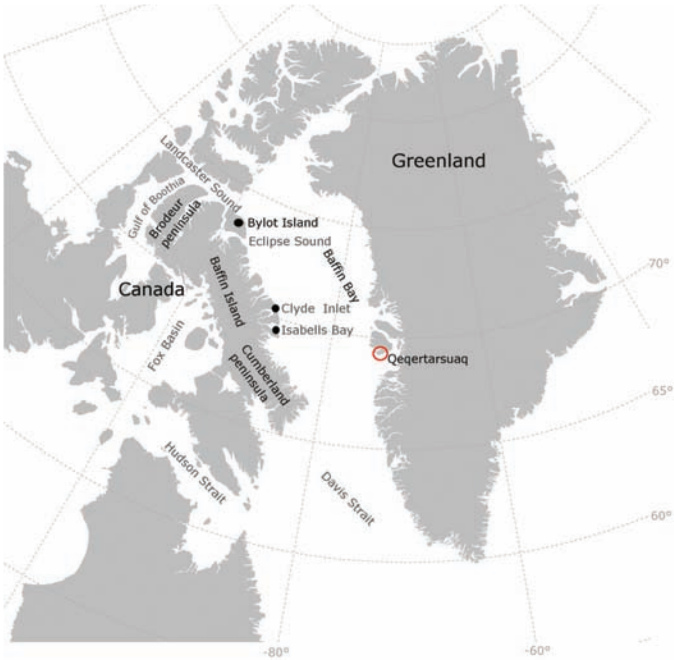

FIG. 1. Study area with locality names and longitude/latitude. Instrumentations took place from dinghies off the coast of Qeqertarsuaq (red circle), West Greenland.

whale, and while the whale was diving, the boats spread out and waited for the whale to reappear. This procedure was repeated until it was possible to get close enough to apply the tag from the boats. Each boat had a custom-made platform from which to perform the tagging using either a custom-made 8 m long fiberglass pole (SPLASH tags; Fig. 2A) or a pneumatic gun (MK10 tags; Fig. 2B) (Heide-Jørgensen et al., 2001, 2006). The behaviour of the whale determined which tag to use. If the whale was calm and allowed a close approach, then a SPLASH tag was used, but if it was difficult to get close to the whale, a MK10 tag was used. A skin biopsy for genetic studies and molecular sex determination was taken from each tagged whale either with the pole or with a crossbow, using genetic methods described in Heide-Jørgensen et al. (2012a). All tags started transmitting shortly after deployment when the conductivity switch was activated during submergence. When a 2009 transmitter ended its transmission before the 2010 field season began, the PTT ID for that particular tag was reused the following year (# 7927, 7929, 7930, 20688, and 20689).

Analyses of Movements

To locate areas of importance to the bowhead whales, we analyzed individual dive behaviour by using geographic positions. Positions were determined from transmitter uplinks received by Argos satellites, and when possible, a single daily average position was calculated. All data from the deployment day and the following day were removed from the dataset in order to prevent data from being biased by the tagging event.

The quality of the location data was determined on the basis of predicted accuracy using seven location classes (Z, B, A, 0, 1, 2, 3, in order of increasing accuracy of position). Locations were filtered using the "Argos filter" algorithm (Freitas, 2012), first described in Freitas et al. (2008). First, the filtering process removed all class Z locations caused by location process failure. The algorithm then removed all locations requiring unrealistic swimming speeds (> 2 ms^{-1}) unless the point was located less than 5 km from the previous location, in which case they were retained. This procedure enabled retention of good-quality locations for which high swimming speed was the result of locations acquired very close to each other in time. The last step filtered out locations where turning angles were larger than 15° in tracks exceeding 2500 m and smaller than 25° in tracks exceeding 5000 m because the greater the turning angle, the less likely it was that the corresponding location represented a real movement.

The daily mean of all positions was used to reduce the number of positions to one per day per individual. Six whales had gaps of 1–35 days between days with positions; however, data on dives were still provided during those gap days. In order to include the dive data from these whales, linearly interpolated positions for days with missing positions were generated by calculating the intermediate positions between the known positions. If only one day was missing, the generated position calculated was halfway between the two known positions. If two days were missing, the first day would be one-third the distance and the second day two-thirds the distance between the two known positions, and so forth. A threshold of a maximum five days with missing locations was accepted, and data sets with longer periods of missing positions were not included.

Analysis of Dive Behaviour

Raw dive data collected by each tag were summarized in four daily six-hour blocks (0000–0600, 0600–1200, 1200–1800, and 1800–2400 UTC). Studies of diving bowhead whales show that feeding rarely occurs near the surface (Richardson et al., 1995), so a dive was defined as a time when the whale was submerged below 10 m (approximately the length of a whale). The dive rate (number of dives per hour) was averaged over each 24 h period to match the time scale of the daily locations. The dives were classified into 12 bins (bin 1 = 2–10 m, bin 2 = 10–20 m, bin 3 = 20–50 m, bin 4 = 50–100 m, bin 5 = 100–150 m, bin 6 = 150–200 m, bin 7 = 200–300 m, bin 8 = 300–400 m, bin 9 = 400–500 m, bin 10 = 500–600 m, bin 11 = 600–700 m, bin 12 > 700 m) within two different dive behaviour categories: percentage time at depth (TAD) and dive depth (m), defined as the mid-range value of each histogram bin. The satellite transmitters also provided one maximum dive depth (m) every 24 hours that was the maximum dive depth for all dives within that period.

Potential foraging areas for bowhead whales were identified in areas where the whales made 2–5 dives h^{-1} over an

FIG. 2. Tagging of bowhead whales from a specially made tower in the stern of a dinghy. A: SPLASH tags were deployed using a custom-made fiberglass pole with a sharp cylinder for obtaining a skin biopsy. B: MK10 tags were deployed with a pneumatic gun, and a crossbow was used to sample a skin biopsy.

average of 24 h. This threshold was based on previous studies that quantified the parameters of foraging dives for bowhead whales in March–June in Disko Bay (Heide-Jørgensen et al., 2013). Overall, foraging dives in Disko Bay lasted on average 883 seconds (≈15 min) regardless of the month. Bowhead whales in Heide-Jørgensen et al. (2013) kept that dive duration regardless of the large shift in dive depth that happened from winter (March-April) to spring (May-June). Keeping a threshold of 2 – 5 dives h^{-1} allows for periods of resting on the surface or other near-surface behaviour. If we assume bowhead whales from the EC-WG stock forage with similar tactics within their whole distribution, we would not expect whales to make more than four foraging dives in a single hour and would not expect those dives to be shallower than 10 m (mean depth of U-shaped foraging dives in Heide-Jørgensen et al. (2013) was reported as 37.8 m). The average number of dives per hour was generated only for animals with an average of 10 or fewer dives h^{-1} during a 24 h period. This limit was set to eliminate occasionally unrealistic numbers of foraging dives (cf. Heide-Jørgensen et al., 2013). To consolidate the predefined threshold for dive rates, we plotted four scenarios of dive rates (≤ 2, ≤ 3, ≤ 4, and ≤ 5 dives h^{-1}) and visualized the density of whales (for more than three whales) in a given area.

The arrival and departure dates for bowhead whales in potential foraging areas were identified for each whale that met the dive rate criteria, and these dates were compared between years. Dive rate, dive depth, and horizontal velocity were calculated and compared within each foraging area, between different foraging areas, and between foraging areas grouped together and all other areas visited by whales (referred to as remaining areas). The software used for analysis was R (R Development Core Team, 2013), including the packages lme4 and multcomp (Hothorn et al., 2008; Bates et al., 2014).

A general linear mixed model (Baayen et al., 2008) was used with individual whales as random effect to investigate the impact of different foraging areas on horizontal swimming velocity, dive rate, and dive depth. To test for differences between foraging areas, post hoc pairwise comparisons were made using Tukey contrasts. The assumption of normal distribution and homogeneous residuals was fulfilled by visually inspecting the residuals against fitted values. Horizontal velocity was log-transformed, and dive rate was square-root transformed. Possible effect on the behavioural response in an identified foraging area compared to the reduced model without the identified foraging areas was tested using a likelihood ratio test. Statistical significance was evaluated at the 5% level.

RESULTS

During the study (2009 – 10), 44 tags were successfully deployed on bowhead whales, and 39 tags (2009: 3 MK10 and 7 SPLASH, 2010: 8 MK10 and 21 SPLASH) provided positions for more than 24 h (Table 1). However, the number of transmitting tags decreased with time, and within the first two months of deployment, nearly 40% of all tags came off, stopped transmitting, or provided no data during transmissions (Table 1). The proportion of whales that transmitted good-quality positions in a day was highest in the months of May and June (average n = 24 whales) after deployment of the tags, and lower from September to December (average n = 5 whales, Fig. 3). The quality of good positions also declined over time (Fig. 3, Table 1). Molecular sex identification from 42 animals revealed that 81% (n = 34) of the whales tagged in Disko Bay in 2009 and 2010 were females and 19% (n = 8) were males.

Movement Patterns and Foraging Areas

Immediately after tagging, all whales remained in the Disko area (incorporating Disko Bay and west of Disko Bay); the latest departure was on 3 June. Duration of tag transmissions differed greatly between the whales (from 6 – 487 days, Table 1). Despite individual variation, overall monthly movement patterns observed on a large scale

TABLE 1. Deployments of 39 satellite transmitters on bowhead whales in Disko Bay, West Greenland, 2009–10.

PTT ID	Type	Deployment date	Last day with contact	Deployment longevity (d)	Sex	Average velocity (ms^{-1})[1]	Average no. of dives per hour (≤ 10 dives)[2]	Average binned dive depth (m)
7929	SPLASH	13-05-2009	12-06-2009	30	F	0.30	N/A[3]	46
20688	SPLASH	13-05-2009	11-06-2009	29	F	0.47	0.30	54
20689	SPLASH	13-05-2009	29-11-2009	200	N/A	0.28	N/A	60
21794	SPLASH	15-05-2009	06-08-2009	83	F	0.40	1.41	42
20158	SPLASH	16-05-2009	17-06-2009	32	F	N/A	N/A	N/A
21800	SPLASH	16-05-2009	17-07-2009	62	M	0.12	0.63	49
21803	SPLASH	16-05-2009	02-07-2009	47	F	0.51	N/A	53
21802	SPLASH	17-05-2009	17-12-2009	214	F	0.30	0.76	72
7927	MK10	25-05-2009	24-12-2009	213	F	0.41	2.68	62
7930	MK10	26-05-2009	23-06-2009	28	M	0.43	0.58	55
20157	MK10	26-05-2009	10-08-2009	76	M	0.36	1.62	58
27261	SPLASH	16-03-2010	02-06-2010	78	F	0.16	1.27	47
37227	SPLASH	17-03-2010	11-05-2011	420	F	0.39	1.99	95
27262	SPLASH	19-03-2010	19-07-2011	487	F	0.33	2.31	86
37282	SPLASH	20-03-2010	20-08-2010	153	F	0.25	2.40	70
27259	SPLASH	22-03-2010	08-05-2010	47	F	0.14	1.10	107
27258	SPLASH	31-03-2010	05-09-2010	158	F	0.44	2.38	53
37228	SPLASH	31-03-2010	28-10-2010	211	F	0.44	2.18	93
42524	SPLASH	31-03-2010	07-08-2010	129	F	0.31	1.88	65
20164	SPLASH	02-04-2010	22-01-2011	295	F	0.38	1.80	61
20165	SPLASH	02-04-2010	26-05-2010	54	F	0.11	N/A	36
20166	SPLASH	02-04-2010	12-08-2010	132	F	0.30	0.48	39
20168	SPLASH	02-04-2010	11-06-2010	70	F	0.18	N/A	29
50687	SPLASH	02-04-2010	26-09-2010	177	F	0.30	2.41	92
3961	MK10	03-04-2010	09-04-2010	6	F	N/A	0.10	128
60005	SPLASH	03-04-2010	30-06-2010	88	F	0.30	1.86	69
7618	MK10	04-04-2010	09-06-2010	66	F	0.23	2.02	82
20683	SPLASH	05-04-2010	13-07-2010	99	F	0.37	N/A	51
20684	SPLASH	05-04-2010	22-04-2010	17	F	0.21	2.73	58
6337	MK10	06-04-2010	13-06-2010	68	N/A	0.18	2.51	33
20685	SPLASH	08-04-2010	25-08-2010	139	F	0.39	N/A	37
7926	MK10	15-04-2010	11-09-2010	149	F	N/A	1.06	77
20688	SPLASH	15-04-2010	03-05-2010	18	M	0.21	0.35	38
7927	MK10	19-04-2010	09-12-2010	234	M	0.36	3.09	98
20689	SPLASH	19-04-2010	02-10-2010	166	F	0.43	0.47	36
20690	SPLASH	20-04-2010	21-06-2010	62	F	0.27	N/A	28
7929	MK10	03-05-2010	06-11-2010	187	M	0.51	3.30	77
7930	MK10	09-05-2010	31-08-2010	114	F	0.36	2.85	136
7934	MK10	10-05-2010	13-10-2010	156	F	0.48	2.91	63

[1] From algorithm in Freitas (2012).
[2] Average number of dives over 24 hours.
[3] N/A = not available.

were similar between years and among individuals (Fig. 4). Three whales ended their transmission in the Disko area, whereas the remaining 36 whales had moved out of the Disko area by 3 June. Those whales followed the continental shelf north off West Greenland towards the northern part of Baffin Bay, where they crossed the bay and went south along the shelf off the east coast of Baffin Island, which they all had reached by 20 July. The whales continued southward and entered Hudson Strait, where contact with the tags was lost in Foxe Basin. Thirty-six whales provided data on horizontal velocity and daily average velocity, which ranged between 0.11 and 0.51 ms^{-1} with an average of 0.32 ms^{-1} (SD = 0.11).

The movements of two female bowhead whales differed notably from the rest. Both whales crossed Baffin Bay directly west of Disko Bay between 67˚N and 68˚N. One whale (#37227) moved north, spent 12 days at Eclipse Sound, and then returned along Baffin Island, where it entered Hudson Strait in late August. It moved through Foxe Basin and the Gulf of Boothia and followed the coast around the Brodeur Peninsula, through Lancaster Sound past Bylot Island, and along the east coast of Baffin Island to Cumberland Peninsula, where it crossed Davis Strait in late April 2011 and ended its transmission northwest of Disko Bay in May 2011 (420 days deployment). The other whale (#27262) started out by taking the same route as #37227, but turned 180˚ when it reached Isabella Bay and followed the east coast of Baffin Island, entered Hudson Strait in late July, and continued to the northern part of Foxe Basin. Instead of continuing through the Gulf of Boothia, it turned around, left Hudson Strait, crossed Davis Strait and returned to west of Disko Bay in April 2011. Thereafter it continued north of Disko Bay, crossed Baffin Bay and ended its transmissions north of Clyde Inlet in late July 2011. For unknown reasons, #27262 did not transmit any data on position between 30 January and 11 April 2010.

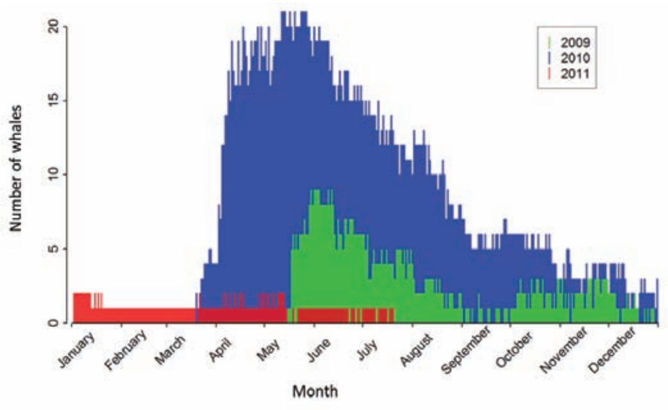

FIG. 3. Distribution of days with good-quality positions (1, 2, and 3) in 2009 (green) and 2010 (blue). Three whales tagged in 2010 continued their transmissions in 2011 (red).

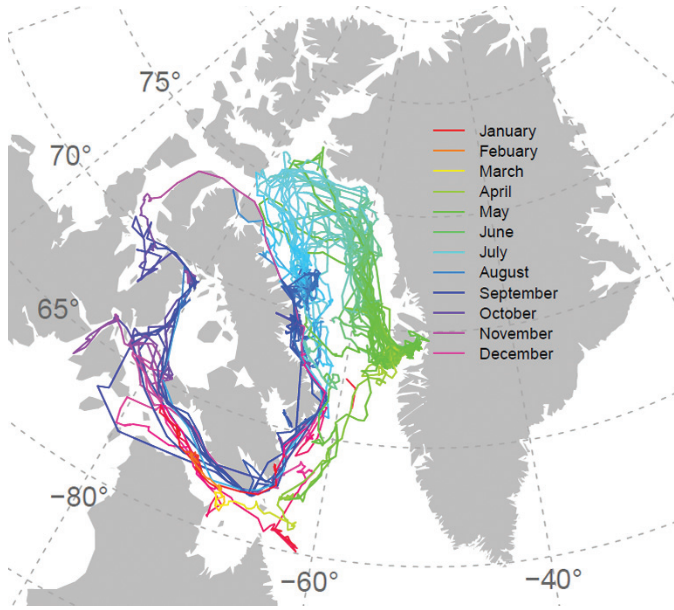

FIG. 4. Monthly movements of 39 bowhead whales satellite-tagged in 2009 and 2010, all deployed off Qeqertarsuaq (Disko Island, West Greenland). Of these 39 whales, 36 moved out of Disko Bay.

Thirty whales provided information on foraging behavior, and potential foraging areas were identified visually for areas where the whales made 2–5 dives h^{-1} over an average of 24 h. (Table 1, Fig. 5). Dive rates of less than 2 dives h^{-1} categorized only Disko Bay as a foraging area, while dive rates of less than 4 and 5 dives h^{-1} provided unrealistically large foraging areas, for example, deep-water ice-covered areas. Dive rates lower than 3 dives h^{-1} visually provided the most realistic number of foraging areas. Nine areas of interest to the bowhead whales were identified (Table 2, Fig. 5).

Within the nine foraging areas identified by fewer than 3 dives h^{-1}, the overall average number of dives ranged from 0.9 to 2.5 dives h^{-1} (mean: 1.7) and was significantly different (df = 9, $p > 0.001$) from the number of dives per hour outside the nine foraging areas (range 7.3 to 29.8 dives h^{-1}; mean: 14.8). Whales dove significantly less in four of the nine identified foraging areas compared to the remaining areas. Differences in dive rate were highly significant in the Disko area and southern Foxe Basin (Tukey, $p < 0.0001$) and less significant in Clyde Inlet and Isabella Bay (Tukey, $p < 0.05$). Average horizontal velocity (ms^{-1}) within the nine foraging areas ranged from 0.21 to 0.49 ms^{-1} (mean: 0.35), which was significantly different from horizontal velocity in the remaining areas (mean 0.41; df = 9, $p > 0.001$, Fig. 6). In four foraging areas (Broughton Island, Disko area, Isabella Bay, and northern Foxe Basin), the horizontal velocity was significantly lower than in the other five foraging areas (Tukey, $p < 0.01$, Table 2).

The most frequently used dive depth (mean: 63.4 m, range: 41.7 to 113.4 m) in the combined foraging areas was shallower than the most frequently used dive depth in the remaining areas (mean: 141.5 m, range: 62.1 to 353 m; df = 9, $p < 0.001$). However, the average binned dive depth (m) in Broughton Island, Cumberland Sound, Disko area, Frobisher Bay, Hudson Strait, Isabella Bay, and southern Foxe Basin was significantly deeper than in the remaining areas (Tukey, $p < 0.0001$). The maximum dive depths (m) within the identified foraging areas were significantly different from those in the remaining areas. Bowhead whales had significantly deeper maximum dives (m) in all identified foraging areas combined, compared to the remaining areas (two-sample t-test $p < 0.0005$). Foraging areas were visited by bowhead whales for an average 119 days (range: 58 to 197 days) before they moved on.

In all of the identified foraging areas, the whales displayed significantly differently behaviour in at least one of the three parameters mentioned above (dive rate, horizontal velocity, or dive depth) compared to the remaining areas. In general, bowhead whales displayed fewer dives, lower horizontal velocity, and deeper dive depths in the identified foraging areas than in the remaining areas.

DISCUSSION

Deployment of satellite transmitters on cetaceans is an important tool for understanding movement and foraging behaviour and for identifying areas of importance. Potential disturbance from tag deployment is believed to be low or of short duration (Heide-Jørgensen et al., 2013); however, to avoid possible tagging effects, data from the deployment day and the following day were discarded. There was no detectable decline in battery voltage in any tags, indicating that other factors, such as failure of the tag itself, improper placement of the tag, or physical impacts (contact with ice or other bowhead whales), probably caused the longevity of the tags to vary. Collection of dive data was restricted to binned records of diving events, and because of the low bandwidth of the Argos Data and Location System, full dive profiles could not be obtained. However, binned data allowed for long-term data collection from areas where it would otherwise be impossible to gather information on diving behaviour of bowhead whales.

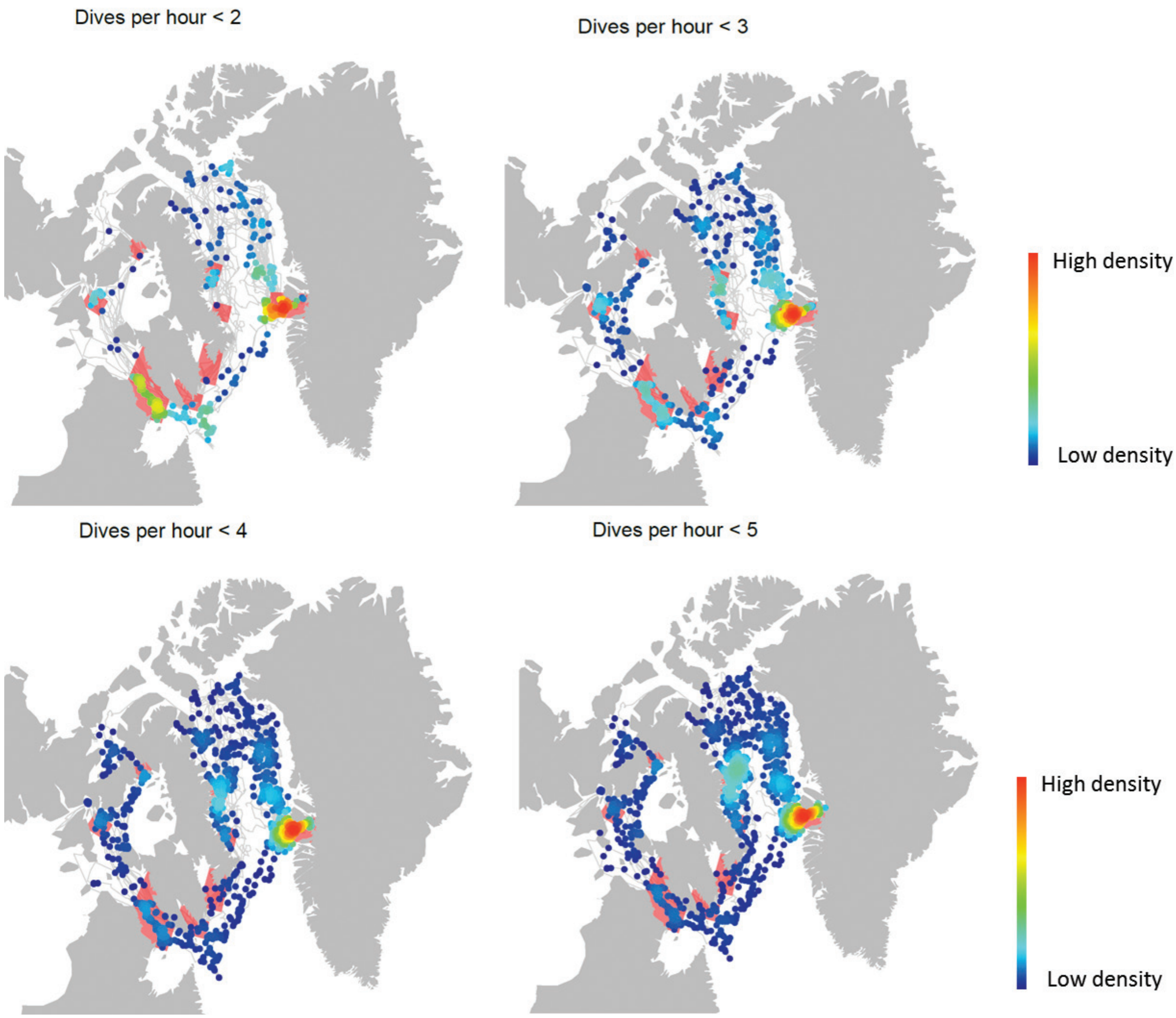

FIG. 5. Potential bowhead whale foraging areas (nine pink areas) assigned by diving rate of 3 dives h^{-1}.

Genetic analysis of skin biopsies from bowhead whales in Disko Bay revealed a large proportion of females (81%) similar to those found in previous studies (Heide-Jørgensen et al., 2010; Wiig et al., 2011; Rekdal et al., 2015). The explanation for the sex segregation remains unresolved although it has been suggested that Disko Bay is used by post-lactating, pregnant, or resting females to regain fat deposits that are otherwise more energetically demanding to acquire in other areas (Heide-Jørgensen et al., 2010). The fact that the data in this study are derived mainly from adult females is important when interpreting the results since juvenile bowhead whales may exhibit different dive and foraging behaviour.

The latest departure date from the Disko area (3 June) is in agreement with both historical and recent studies (Eschricht and Reinhardt, 1861; Heide-Jørgensen et al., 2003a, 2006; Laidre and Heide-Jørgensen, 2012). The departure date in the beginning of June coincides with the peak density of copepods in the water column in Disko Bay (Madsen et al., 2001) and the early departure of bowhead whales, which rely on large quantities of copepods, seems counterproductive unless the whales are targeting swarms of overwintering copepods located close to the bottom rather than the less dense copepod concentrations in the water column that appear in June (Heide-Jørgensen et al., 2013). Copepods are aggregated near the seabed during their winter diapause and in spring migrate vertically in the water column. As they reach the upper layers (< 50 m), copepods become more scattered as a result of variability in hydrography (e.g., wind and currents), which may be why it is more efficient for bowhead whales to target swarms of copepods at lower depths (Laidre et al., 2007). Ashjian et al. (2010) suggested similar drivers for bowhead whales feeding on krill near Barrow, Alaska. Laidre et al. (2007) did

TABLE 2. Nine areas assigned as potential foraging areas for bowhead whales and identified in Figure 5. The Disko area includes Disko Bay and the area west of Disko Bay. The remaining areas are all other areas visited by the bowhead whales.

Potential foraging area	Number of whales	Days with positions	Earliest arrival date	Latest departure date	Average horizontal velocity (ms^{-1})	Average no. of dives h^{-1} (24 h)		Average binned dive depth (m)		Maximum dive depth (m)	
						> 3 h^{-1}	≤ 3 h^{-1}	> 3 h^{-1}	≤ 3 h^{-1}	> 3 h^{-1}	≤ 3 h^{-1}
Disko area	39	130	19 March[1]	3 June	0.21	20.5	2.5	87.6	61.6	610	688
Clyde Inlet	12	33	19 July	8 November	0.41	8.6	2.3	88.4	47.6	390	364
Isabella Bay	11	85	1 August	10 November	0.25	16.4	2.2	142.2	87.8	382	450
Broughton Island	9	60	8 June	26 November	0.30	11.1	1.6	350.0	74.9	514	484
Cumberland Sound	10	78	31 July	12 December	0.42	29.8	0.9	144.5	92.8	640	378
Frobisher Bay	8	36	18 July	2 January	0.49	25.2	2.0	143.8	114.3	438	258
Hudson Strait	7	106	21 July	3 March	0.49	7.3	0.9	130.7	42.6	454	274
Southern Foxe Basin	5	54	5 September	2 November	0.33	9.1	1.2	246.6	21.7	430	na
Northern Foxe Basin	3	65	31 July	25 October	0.28	4.9	1.5	23.9	44.7	216	198
Remaining areas	27	585	–	–	0.41	15.4	1.6	57.5	49.7	610	444

[1] Date of first deployment.

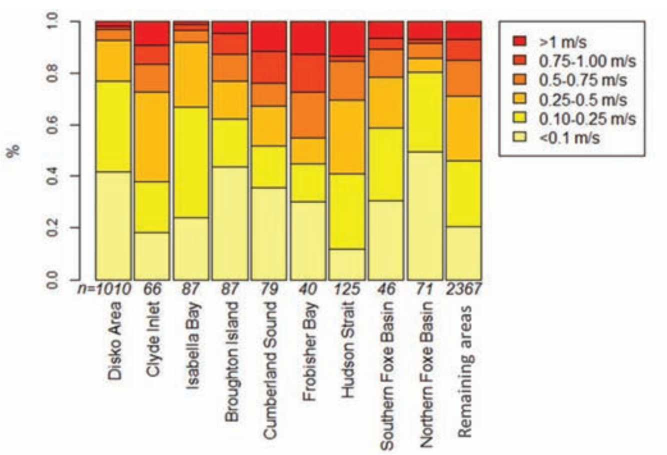

FIG. 6. Average horizontal velocity of the whales in the nine potential foraging areas.

not find a correlation between bowhead whale dive duration and dive depth in Disko Bay, which might indicate that bowhead whales from West Greenland forage with similar dive rates throughout their distribution. Bowhead whale dive depth and duration have been correlated in the Beaufort and Chukchi Seas, but only for dives of 1 min or less and in depths of 16 m or less (Krutzikowsky and Mate, 2000).

The identification of foraging areas was determined from an important biological parameter: the dive rate of the bowhead whales. The threshold of about three dives per hour was based on the average time bowhead whales spend on foraging dives in Disko Bay, West Greenland (Heide-Jørgensen et al., 2013). The sensitivity of a fixed threshold of three dives per hour was examined by including areas with two to five dives per hour. Localities with more than three dives per hour included transient areas that are unlikely to be important as feeding areas (e.g., offshore pack-ice areas over deep water). The use of a low threshold value for the hourly number of dives is also supported by the basic assumption that an obligate filter feeder must optimize its dive time (= fewer dives per hour) to benefit maximally from high-density prey concentration. Surface skim feeding has been observed by Moore et al. (2010) near Barrow, Alaska, where euphausiids and copepods near the shelf break are advected onto the shelf northeast of Point Barrow under certain wind conditions (Citta et al., in press). This retention and aggregation of zooplankton on the shelf was referred to as the "krill trap" by Ashjian et al. (2010). There are no similar oceanographic conditions or congregations of krill in the Baffin Bay and adjacent waters, and skim feeding has not been described so far for this area.

Feeding at or close to the surface (i.e., skim feeding) was not detected in this study because the depth threshold for feeding dives was set at 10 m, but this type of feeding is generally hard to distinguish from shallow submergence during swimming. However, there is no evidence from Baffin Bay and adjacent waters of large zooplankton concentrations above the 10 m depth that could support skim feeding. The maximum dive depth (m) was significantly deeper in areas identified as foraging areas than in all other areas the bowhead whales visited. This result indicates that bowhead whales most likely perform deeper dives in areas where they are foraging than in areas not used for foraging, which is also in agreement with Figure 5.

Data from whales instrumented in this study indicate that bowhead whales tracked from Disko Bay show similar broad-scale dispersal patterns and dive behaviour. On a smaller scale, however, movement behaviour was variable. Bowhead whales are highly adapted to dense sea ice (Mate et al., 2000; Heide-Jørgensen and Laidre, 2004), and satellite tracks from bowhead whales tagged in 2002 and 2003 in Disko Bay show a straight line through dense sea ice to the northwestern part of Baffin Bay (Heide-Jørgensen et al., 2003a, 2006). However, bowhead whales in this study moved along the coast of West Greenland before crossing the northern part of Baffin Bay. Satellite images of Baffin Bay in June 2002, 2003, 2009, and 2010 showed no apparent differences in sea ice cover between years (DMI, 2014) that could explain the difference in movement patterns of bowhead whales. Both Inuit hunters and commercial whalers also noted variation in movement between years (Southwell, 1898).

Bowhead whales are known to be able to perform prolonged dives at a low velocity when foraging, and the overall low average horizontal velocity (0.38 ms^{-1}) within the entire range was in agreement with other observations (Heide-Jørgensen et al., 2003a) and emphasizes that bowhead whales are slow swimmers (Simon et al., 2009). Whales did not spend 100% of their time feeding in foraging areas, and they most likely also exhibit other types of behaviour, such as social interaction, nursing of calves, resting, or interaction with dense ice.

The diving behaviour of the instrumented whales in this study offers insight into foraging areas used by bowhead whales, and some of the foraging areas identified in this study were also identified in other studies using other methods. The Disko area, Isabella Bay, Cumberland Sound, Frobisher Bay, and Hudson Strait are areas that previously have been identified as important to bowhead whales on the basis of whaling, behavioural observations, and sightings from surveys (Finley, 1990; Heide-Jørgensen et al., 2006; Wheeler et al., 2012). However, this study identified additional areas in the southern and northern part of Foxe Basin, Broughton Island, and Clyde Inlet, areas not included as high-suitability areas by Wheeler et al. (2012).

Bowhead whales visited several areas, suggesting flexible use of foraging areas. Rather than holding to strict foraging patterns or migration routes, bowhead whales apparently have more elastic behaviour when compared to the two other Arctic cetaceans, narwhals (*Monodon monoceros*) and belugas (*Delphinapterus leucas*) (Richard et al., 1998; Dietz et al., 2001; Heide-Jørgensen et al., 2003b, c). This flexibility may favour bowhead whales with regard to impacts of climate change on their habitats. Foote et al. (2013) suggested that bowhead whales in the North Atlantic will face a major reduction in their potential habitat range with the continued decline in sea ice distribution and speculated that the stock will face severe population consequences. The present study indicates that bowhead whales in the North Atlantic use a wide range of habitats that extend far into the Canadian Arctic Archipelago, including large areas not considered in the predictions by Foote et al. (2013). Fossils of bowhead whales dating back to the early Holocene (between 4000 and 7500 BP) have been located as far north as Axel Heiberg Island and Ellesmere Island, which suggests that bowhead whales were able to exploit a much larger area during the period of milder climate (and lack of sea ice) in the early Holocene (Bednarski, 1990; Dyke and England, 2003). Zooplankton are highly linked to the bloom of the phytoplankton community, and it has been suggested that reduced sea ice cover entails an early bloom of phytoplankton, thereby diminishing the foundation for the zooplankton community (Søreide et al., 2010). A reduction in sea ice cover may increase prey availability for bowheads (Moore and Laidre, 2006; Wheeler et al., 2012), thereby benefiting the species, at least initially, in a warmer Arctic.

Areas that are known to be important for feeding (e.g., Isabella Bay and the Disko area) are also visited by whales that show no signs of foraging activity (using measurable dive and velocity metrics). Bowhead whales must target large densities of zooplankton when foraging, but zooplankton communities are often patchy (Folt and Burns, 1999) and may not always be accessible. Bowhead whales likely have to be efficient when it comes to energetic maintenance and rely on energy stored in the blubber. This energy storage, together with low energetic costs associated with normal metabolic activity, acts as a buffer against environmental instability and likely allows some bowhead whales to survive long periods without intensive foraging. It may also allow whales to traverse large areas at little energetic cost. In terms of population consequences, bowhead whales may be sufficiently flexible with large environmental tolerances to sustain moderate (and predicted) changes in the Arctic.

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