



# Age- and sex-specific movement, behaviour and habitat-use patterns of bowhead whales (*Balaena mysticetus*) in the Eastern Canadian Arctic

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Received: 23 October 2019 / Revised: 23 August 2020 / Accepted: 27 August 2020 / Published online: 3 October 2020  
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## Abstract

As an annual ice-associated species, bowhead whales (*Balaena mysticetus*) are known to move northward in mid-to-late March and southward in early winter while following the annual cycle of sea ice decay and formation. We sought to determine when and where different demographic groups of Eastern Canada-West Greenland bowhead whales foraged throughout their range and what seasonal patterns occurred in their migratory and residency behaviour over a 16-year time period (2001–2016). Fifty-nine bowhead whales were equipped with satellite telemetry tags and hierarchical switching-state-space models (HSSSM) were used to infer probable foraging and travelling behaviour. Overall, 18,294 locations were predicted with the HSSSM and 70% of the locations ( $n = 12,784$ ) were associated with probable foraging behaviour and 15% ( $n = 2709$ ) included movements consistent with travelling behaviour. Both males and females were found to reside in Hudson Strait during winter. Females showed a slight preference for more northern regions (e.g. Gulf of Boothia) for feeding during summer compared with males who appeared to spend more time in more southern foraging grounds (e.g. Cumberland Sound). Females in Gulf of Boothia were significantly larger than females in Cumberland Sound but males were of comparable sizes in both regions. Lancaster Sound had the lowest occupancy, representing less than 0.8% of all HSSSM locations ( $n = 154$ ) suggesting that this area may not be preferred by subadult male or female bowhead whales. Understanding whale movement behaviour will assist in anticipating patterns in distribution shifts associated with warming.

**Keywords** *Balaena mysticetus* · Seasonal movement · Habitat use · State-space modelling · Foraging · Satellite telemetry

## Introduction

Determining what influences movements and habitat-use patterns and how they are changing over time is particularly important for Arctic marine species, such as bowhead whales (*Balaena mysticetus*) that are having to adjust to considerable fluctuation in environmental conditions (e.g. Stroeve et al. 2007, 2017; Notz and Stroeve 2016). There are several factors known to influence marine mammal distribution at both the individual and population level, including: habitat conditions (e.g. physical and environmental such as sea ice cover; Keller et al. 2006; Higdon and Ferguson 2010;

Gregg et al. 2013), biological constraints (e.g. prey availability, presence of predators; Kenney et al. 2001; Hlista et al. 2009; Moore et al. 2010; Reinhart et al. 2013), demography (e.g. population size and demographic rates; Cosens and Blouw 2003; Heide-Jørgensen et al. 2010), species adaptations (e.g. morphological, physical and behavioural; Ford and Reeves 2008), and interactions with humans (e.g. disturbance and pollution; Robertson et al. 2013). Although some factors are likely to be more important than others, the relative importance of each factor is poorly understood given the logistical challenges associated with studying long-term patterns in Arctic cetacean movement and habitat use.

Our current understanding of bowhead whale distribution and habitat use has come largely from systematic aerial and boat-based surveys and satellite telemetry studies. Due to weather constraints, systematic surveys have been generally limited to determining spring and summertime whale aggregations. Logistical and financial constraints also limit the area that can be surveyed and thus tend to yield low spatial resolution. Although informative, the low temporal

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resolution of survey data has resulted in little knowledge about bowhead whale seasonal movements and distribution during fall and winter. Satellite telemetry has helped fill in these gaps by providing detailed information about the seasonal and interannual movement of individual animals.

Satellite telemetry studies have shown that bowhead whales are widely distributed throughout the Eastern Canadian Arctic and that they make long, seasonal migrations that correspond to spatio-temporal changes in sea ice conditions (Heide-Jørgensen et al. 2003; Laidre et al. 2007; Ferguson et al. 2010; Pomerleau et al. 2011a). During winter, individuals belonging to the Eastern Canada-West Greenland (ECWG) bowhead whale population typically reside in Hudson Strait, northern Hudson Bay, east Baffin Island and along the ice edge of West Greenland (Reeves and Heide-Jørgensen 1996; Koski et al. 2006). Animals are then found along the west coast of Greenland, and the Eastern and southern coasts of Baffin Island in Cumberland Sound and Foxe Basin, and in Lancaster Sound during spring (Ferguson et al. 2010; Pomerleau et al. 2011b). Concurrent with the annual minimum sea ice cover during summer, animals generally expand their poleward range, occupying northern fiords and bays in the Canadian High Arctic (such as the Gulf of Boothia; Pomerleau et al. 2011a, b) and occasionally more southern waters such as Hudson Bay and Foxe Basin (Cosens et al. 1997; Cosens and Innes 2000; Ferguson et al. 2010; Higdon and Ferguson 2010). However, during winter when sea ice cover has reached its annual maximum, the whales concentrate along the southern edge of their range as ice forms (e.g. Hudson Strait).

Bowhead whale foraging areas have been identified by using hierarchical switching-state-space models (HSSSMs) to quantitatively infer behaviour from tagged whale tracks. These state-space models (Pomerleau et al. 2011a; Fortune et al. 2020) along with other analyses of movement data (Nielsen et al. 2015; Chambault et al. 2018) and longitudinal stable isotope analysis from baleen (Matthews and Ferguson 2015; Pomerleau et al. 2018) have shown that bowheads forage throughout their range in the Eastern Canadian Arctic and during all times of year. Summertime foraging appears to be particularly important in Cumberland Sound, Prince Regent Inlet, Gulf of Boothia, and Lancaster Sound, Nunavut (Ferguson et al. 2010; Pomerleau et al. 2011a; Nielsen et al. 2015; Fortune 2018), whereas wintertime foraging appears to occur almost exclusively in Hudson Strait (Reeves and Heide-Jørgensen 1996; Koski et al. 2006).

Photogrammetry and biopsy studies have shown that ECWG bowhead whales are known to segregate based on age and sex throughout the Eastern Canadian Arctic (Cosens and Blouw 2003; Heide-Jørgensen et al. 2010). However, little is known about demographic specific (e.g. juvenile, subadult, adult male and female) habitat preferences and temporal variations in bowhead whale habitat-use patterns,

which likely reflect seasonal and interannual variation in prey quality and quantity. These gaps in knowledge may be addressed by increasing sample sizes of long-term movement data to include animals of various sizes (and thus age classes) and sexes.

We used quantitative movement models to study the behaviour, distribution and area-use patterns of bowhead whales in the Eastern Canadian Arctic equipped with long-term satellite telemetry tags. We also explored seasonal patterns in bowhead behaviour (travelling and area-restricted movement) and area use for animals with long tag attachment times, and compared the residency patterns of different demographic groups within the same regions. Our objectives were to identify seasonally important areas for bowhead whales in the Eastern Canadian Arctic, and determine age and sex-specific movement and inferred feeding throughout their range.

## Materials and methods

To understand the long-term movements and area-use patterns of different demographic groups (i.e. age-sex groups) of ECWG bowhead whales, we equipped 59 animals with long-term satellite telemetry tags (Wildlife Computers SPOT and SPLASH MK10). The tags were attached with ~ 20 cm stainless steel anchors and skin and blubber samples were simultaneously collected using 4 cm biopsy tips. The anchors and biopsy tips were sterilized with 1:10 bleach/water solution prior to use and only penetrated the animals' skin and blubber. Biopsy samples were collected to genetically determine sex and to differentiate individuals. The tags were deployed from a wooden canoe freighter using an 8 m fibreglass hand-held tagging pole. The tags were attached dorsally and behind the blow holes to improve data transmission by maximizing the time the transmitter was out of water during a surfacing event.

The whales were tagged in Foxe Basin, Cumberland Sound and Admiralty Inlet during summer from 2001 to 2016 (Table 1). Four of the whales (1 female and 3 unknown sex) were tagged in Admiralty Inlet from 2008 to 2009. The majority of whales were tagged in Cumberland Sound from 2006 to 2016 ( $n=28$ ) (13 female, 13 male and 2 unknown). Twenty-seven whales were tagged in Foxe Basin from 2001 to 2013 (16 female, 9 male and 2 unknown). Juvenile, subadult and non-lactating adult animals were selected for tagging, which meant excluding animals < 8.5 m long and those in mother–calf pairs.

The satellite telemetry tags provide information on date, time, and location of the animal. To record annual movements of individuals, longevity of the tags was increased by programming the Platform Transmitter Terminals (PTTs) to transmit up to 400 times a day during summer, and less

**Table 1** Summary information for Eastern Canada-West Greenland bowhead whales tagged with Wildlife Computers SPOT and SPLASH Tags (MK10) between 2001 and 2016 after removing improbable locations based on swim speed using the vmask function

PTT	Year	Region	Sex	Length	Start	End	Duration
24640	2001	FB	F	NA	07/02/2001	07/10/2001	8
13280	2002	FB	M	1300	07/01/2002	07/20/2002	19
20685	2002	FB	M	1200	07/02/2002	09/29/2002	89
37227	2002	FB	F	1500	07/10/2002	08/22/2002	43
37228	2002	FB	F	1400	07/10/2002	11/08/2002	121
24641	2003	FB	F	1100	07/05/2002	08/23/2002	49
66351	2006	CS	F	1000	07/05/2006	08/09/2006	35
66352	2006	CS	F	1100	07/05/2006	04/23/2007	292
66353	2006	CS	M	1200	07/05/2006	05/12/2007	311
66354	2006	CS	M	1300	07/05/2006	08/09/2006	35
66355	2006	CS	NA	1350	07/05/2006	12/13/2006	161
66356	2006	CS	M	1200	07/05/2006	02/09/2007	219
66357	2006	CS	NA	NA	07/05/2006	07/14/2006	9
66358	2006	CS	M	900	07/11/2006	01/25/2007	198
66359	2006	CS	F	1300	07/05/2006	05/26/2007	325
39146	2008	AI	F	NA	08/16/2008	09/04/2008	19
39172	2009	AI	NA	1000–1200	08/18/2009	08/18/2009	0
39223	2009	AI	NA	1200–1350	08/16/2009	08/27/2009	11
39226	2009	AI	NA	1000–1200	08/16/2009	09/01/2009	16
40153	2011	FB	F	1680–1830	07/10/2011	07/29/2011	19
51867	2011	FB	F	1220	07/09/2011	08/01/2011	23
57600	2011	FB	F	1370–1520	07/08/2011	08/01/2011	24
39161	2012	FB	F	1200	07/19/2011	07/28/2012	375
114494	2012	FB	F	1200	08/13/2012	05/04/2013	264
114495	2012	FB	F	1100–1200	07/03/2012	06/26/2014	723
114496	2012	FB	F	1100	07/03/2012	12/13/2013	528
114497	2012	FB	M	1200	07/06/2012	05/10/2013	308
114498	2012	FB	M	1100	07/06/2012	01/08/2013	186
114499	2012	FB	F	1300–1400	07/06/2012	06/09/2013	338
114500	2012	FB	M	1200–1300	07/07/2012	02/19/2014	592
114501	2012	FB	NA	NA	07/07/2012	01/06/2013	183
114502	2012	CS	M	1000	08/06/2012	07/11/2013	339
114503	2012	CS	F	1000	08/06/2012	12/31/2013	512
114504	2012	CS	F	1000–1100	08/08/2012	07/18/2013	344
114505	2012	CS	M	1100–1200	08/08/2012	06/23/2013	319
114506	2012	CS	F	1300–1400	08/08/2012	08/27/2012	19
114507	2012	CS	M	1000	08/14/2012	09/18/2013	400
114508	2012	CS	M	900–1000	08/12/2012	08/19/2014	737
114509	2012	CS	M	900–1000	08/12/2012	05/27/2013	288
94542	2012	CS	F	900–1000	08/30/2012	11/08/2012	70
94545	2012	CS	M	1300–1400	06/30/2012	10/20/2012	112
128145	2013	FB	F	1100–1200	06/28/2013	11/13/2014	503
128146	2013	FB	F	1300–1400	06/28/2013	05/22/2015	693
128148	2013	FB	F	1300	07/07/2013	05/20/2014	317
128149	2013	FB	NA	1200–1300	07/10/2013	07/22/2013	12
128150	2013	FB	F	1000	07/10/2013	07/08/2015	728
128151	2013	FB	M	900–1000	07/10/2013	07/01/2015	721
128152	2013	FB	M	900–1000	07/10/2013	05/24/2015	683
128153	2013	FB	M	1200	06/28/2013	07/15/2014	382
128154	2013	FB	M	1100–1200	06/29/2013	05/18/2014	323
148499	2016	CS	M	900	09/05/2016	09/29/2016	24

**Table 1** (continued)

PTT	Year	Region	Sex	Length	Start	End	Duration
148500	2016	CS	F	900	08/20/2016	09/13/2016	24
148502	2016	CS	M	900	08/24/2016	09/30/2016	37
148503	2016	CS	F	1000	08/24/2016	09/29/2016	36
148504	2016	CS	F	850–900	08/24/2016	09/30/2016	37
148505	2016	CS	M	1000	08/26/2016	09/30/2016	35
148506	2016	CS	F	1000	08/27/2016	09/15/2016	19
126499	2016	CS	F	1100	08/28/2016	09/30/2016	33
126500	2016	CS	F	1000	08/29/2016	09/30/2016	32

*PTT* is the Platform Transmitter Terminal and is a unique identifier for individual animals. *Year* is the year the animal was tagged. *Region* is the area the individual was tagged and includes Foxe Basin (FB), Cumberland Sound (CS) and Admiralty Inlet (AI). *Sex* was determined for individuals based on biopsy sample collection. *Length* was visually estimated from the vessel based on the distance between the tip of the rostrum and fluke notch of the animal and is expressed in centimeters. *Start* is the first day of location data and *end* is the last day of location data. *Duration* is the time in days between the first and last Argos location

frequently during winter (100 times every second day). Due to the wide distribution of bowheads throughout the Eastern Canadian Arctic and their seasonal selection for sea ice, we used a previously determined definition of seasons that incorporates the seasonal movement of ECWG bowhead whales relative to the sea ice (Ferguson et al. 2010). Consequently, our analysis designated summer when there is near complete absence of sea ice as occurring between 27 June to 27 December, winter between 28 December and 15 March when there is near complete sea ice cover and spring between 16 March and 26 June when sea ice is in a transitional phase and in the process of receding and mating and calving occur (Nerini et al. 1984; Ferguson et al. 2010).

Bowhead body lengths were visually estimated from the tagging vessel and reported as the straight-line distance between the rostrum and the fluke notch. In instances of uncertainty, lengths were recorded as a range and for our analysis, we used the median length (m). We combined information on sex and estimated body length to infer the age classes of tagged animals using published age class-length data (Koski et al. 1993; George et al. 2004; Higdon and Ferguson 2010) whereby male and female juveniles were  $\geq 5.8$  m and  $< 10$  m, probable female subadults were  $\geq 10$  m and  $< 13$ , male subadults were  $\geq 10$  m and  $< 12.5$  m, adult females were  $\geq 13$  m, and male adults were  $\geq 12.5$  m.

### Horizontal movement analysis

The raw Argos data were processed with the least-squares (LS) algorithm. The LS filtered data were subsequently run through a speed filter using the *vmask* function in the *argosfilter* package (Freitas et al. 2008) in R (R Development Core Team 2016). This function filters Argos satellite tracking data and is especially designed for marine animals where location quality is typically poor. For example, of the location quality classes for 59 tagged animals, 0 = 8%,

1 = 7%, 2 = 4%, 3 = 2%, A = 26%, B = 53% and Z = 0.3%. We used a speed threshold of 2 m/s<sup>1</sup> and Argos locations that resulted from swimming speeds above this threshold were subsequently removed from our analysis as they were deemed to be biologically improbable.

We fit a hierarchical switching-state-space model (HSSSM) (Developed by: Jonsen et al. 2005, 2013) to our filtered telemetry data to (1) predict the movement of individual animals, (2) determine an individuals' behavioural state, (3) make population level inferences and (4) standardize the number of locations per animal per day. The *bsam* package in R (R Development Core Team 2016) provided in the supplement of Jonsen et al. (2013) was used to fit a correlated random walk model (CRW) that switched between two CRWs that reflected 'area-restricted movement' and 'travelling' behavioural states (Jonsen et al. 2005). The two CRWs and the associated behavioural states differ in mean turn angle and swimming speed (Jonsen et al. 2005), whereby 'area-restricted movement' reflected instances of low swimming speeds and high turning angles (typical of animals that are searching for and/or consuming prey) and 'travelling' consisted of faster, more linear movements (typical of animals conducting seasonal migrations). The model (HSSSM) was fit to each dataset ( $n = 43$ ) containing a minimum of 28 days of individual-specific location data with a total of 40,000 Monte Carlo Markov Chain (MCMC) iterations, dropping the first 30,000 (i.e. burn-in) and retaining every 10th sample from the remaining 10,000, resulting in a total of 1,000 samples per chain ( $n = 2$  chains).

The HSSSM modelling approach yields regularly spaced location estimates and categorizes behaviour (probable area-restricted movement or travelling). Behavioural states (*b*) were classified based on mean estimates from the MCMC samples, which assumed that  $b = 1$  was travelling and  $b = 2$  was area-restricted movement. We used the same behavioural probability cut-off points as

previous studies (Silva et al. 2014) and locations with mean estimates of  $b > 1.75$  were assumed to indicate area-restricted movement (i.e. probable foraging behaviour);  $b < 1.25$  reflected travelling behaviour; and values between  $b \geq 1.25$  and  $b \leq 1.75$  were unclassified. We then filtered the HSSSM locations (hereafter referred to as locations) based on latitudes and longitudes of previously identified areas of interest for ECWG bowhead whales (i.e. regions) that covered the entire range of the tagged animals in the Eastern Canadian Arctic.

We investigated whether there were regional, body length, sex, age class, and seasonal impacts on occupancy time (i.e. number of days spent in an area) using linear mixed-effects models with the lme statistical package in R (R Development Core Team 2016). We filtered the HSSSM predicted data to include animals that spent a minimum of 10 days within a particular region and season because we were interested in what factors influence bowhead whale area selection and thus did not want to include instances where a tagged whale spent only a short time in an area (e.g. indicative of area exploration and not selection). We assigned minimum and maximum latitude and longitude values to each region based on their geographical obstacles, typically large islands (Table 2). Since individual animals occupied several regions (i.e. repeated measures), we used a mixed-effects model to account for non-independence by including individual animal PTTs as a random factor (Pinheiro and Bates 2000). Several linear mixed-effects models were fit to the summary HSSSM data (i.e. number of days spent in an identified area by animal and season). We used likelihood ratio tests to examine how region, body length, sex, and time of year (summer, winter, or spring) affected bowhead whale occupancy. The Akaike's information criterion (AIC) was used to indicate model support whereby the model with the smallest AIC was deemed to be the "best model."

## Results

Transmission times for the 59 tagged Eastern Canada-West Greenland bowhead whales varied from 0 to 737 days (Table 1) with a mean of 225 days ( $\pm 230.6$  SD,  $n = 13,302$ ). Of the tagged animals, 30 were female, 22 were male, and 7 were of unknown sex. Genetic analysis revealed that no animals were tagged more than once. There were estimates of body length for 90% of the tagged animals ( $n = 53$ ) (Fig. 1). After running the HSSSM, which predicted two daily locations for animals with  $> 28$  days of Argos data and removing predicted locations that resulted from  $> 4$  consecutive gaps in Argos locations, we obtained 18,294 locations for 43 individuals. On average, the tags transmitted for 297 days ( $\pm 226$  SD,  $n = 1543$ ) for animals with  $> 28$  transmission days, providing seasonal information about individual animal movements and area use patterns.

The majority of predicted locations occurred during summer (27 June to 27 December) 58.96% (58.6 locations/day  $n = 10,786$ ) followed by spring (16 March to 26 June) 21.14% (37.5 locations/day;  $n = 3867$ ) and winter (28 December to 15 March) 19.90% (34.7 locations/day;  $n = 3641$ ) of total locations. Overall, we found that 15% ( $n = 2709$ ) of all predicted locations were associated with travelling behaviour (i.e. faster and more linear swim directions), 70% ( $n = 12,784$ ) were consistent with area-restricted movement (ARM) behaviour where animals exhibited slower swim speeds with more tortuous swim paths, indicative of foraging activities. The remaining 15% ( $n = 2801$ ) of locations were associated with an unknown behavioural state.

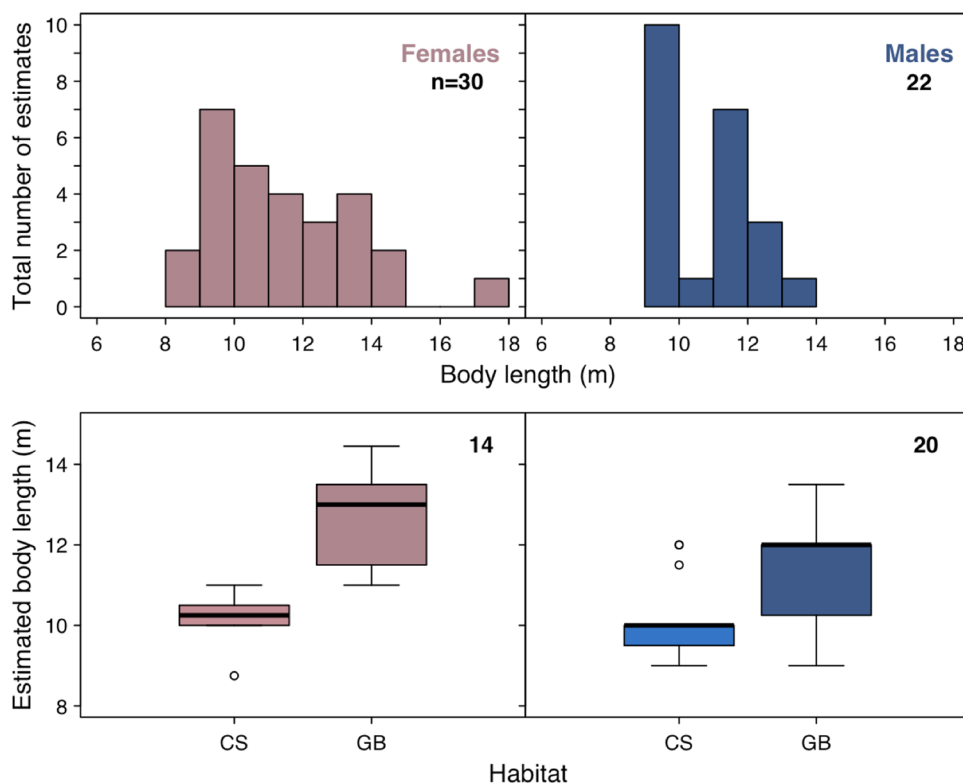
We found seasonal differences in area-restricted movement behaviour whereby, 53.21% (37.17 locations/day;  $n = 6803$ ) of all ARM locations occurred during summer followed by 24.58% (29.93 locations/day;  $n = 3143$ ) in winter and 22.19% (27.55 locations/day;  $n = 2838$ ) in spring. Predicted locations associated with travelling behaviour were most prevalent during summer 76.59% (11.28 locations/day;

**Table 2** Latitude and longitude (decimal degrees) criteria used to filter HSSSM predicted locations by region in the Eastern Canadian Arctic

Region	Latitude min (>)	Latitude max (<)	Longitude min (>)	Longitude max (<)
Cumberland Sound	64.00	67.00	- 67.00	- 63.50
East Baffin Island	66.55	70.00	- 76.00	- 58.00
Foxe Basin	64.80	71.00	- 83.00	- 71.50
Gulf of Boothia, Prince Regent Inlet, Admiralty Inlet	66.50	73.50	- 93.50	- 85.00
Hudson Bay	55.00	64.00	- 95.00	- 78.50
Hudson Strait and Frobisher Bay	57.00	64.20	- 78.00	- 65.00
Lancaster Sound	73.50	85.00	- 90.00	- 77.00

Locations that were greater than the minimum latitude (Latitude min), less than the maximum latitude (Latitude max), greater than the minimum longitude (Longitude min), and less than the maximum longitude (Longitude max) were assigned to a particular region

**Fig. 1** Top panel: Median body lengths (m) of tagged bowheads based on visual estimation of the distance between the tip of the rostrum and the fluke notch for males and females. Sex was determined from genetic analysis of biopsy samples. Bottom panel: Estimated body length (m) measurements for male and female bowhead whales that occurred in Cumberland Sound (CS) and Gulf of Boothia (GB) for a minimum of 10 days during summer



$n = 2075$ ), followed by spring 18.89% (4.97 locations/day;  $n = 512$ ) and winter 4.50% (1.16 locations/day;  $n = 122$ ). Furthermore, to gain insight regarding the seasonality of migration and foraging, we examined temporal patterns in the total number of days of HSSSM locations associated with ARM and travelling by month for 43 tagged whales (Fig. 2). ARM occurred across all months but was greatest during January ( $n_{\text{days}} = 28.56$ ) when ice cover is substantial and lowest in July ( $n = 14.90$ ) during the open water season. Conversely, travelling was greatest during July ( $n_{\text{days}} = 13.12$ ) and lowest in March ( $n_{\text{days}} = 1.60$ ) (Fig. 2).

### Horizontal behaviour by sex

When separating the predicted locations associated with area-restricted movement behaviour by sex (Fig. 3), we found that 47.1% ( $n = 6024$ ) of all locations belonged to 18 females (one female had no ARM-associated locations). Furthermore, 6% ( $n = 1$ ) of the females with ARM locations were from probable juveniles, while 61% ( $n = 11$ ) were probable subadults, and 33% ( $n = 6$ ) were adult females. Overall, 50.7% ( $n = 6485$ ) of the ARM locations were from males ( $n = 19$ ). Of these tagged males, 26.3% ( $n = 5$ ) were probable juveniles, 57.9% ( $n = 11$ ) were likely subadults and 15.8% ( $n = 3$ ) were probable adults. Consequently, the ARM locations consisted mostly of subadult males and females and

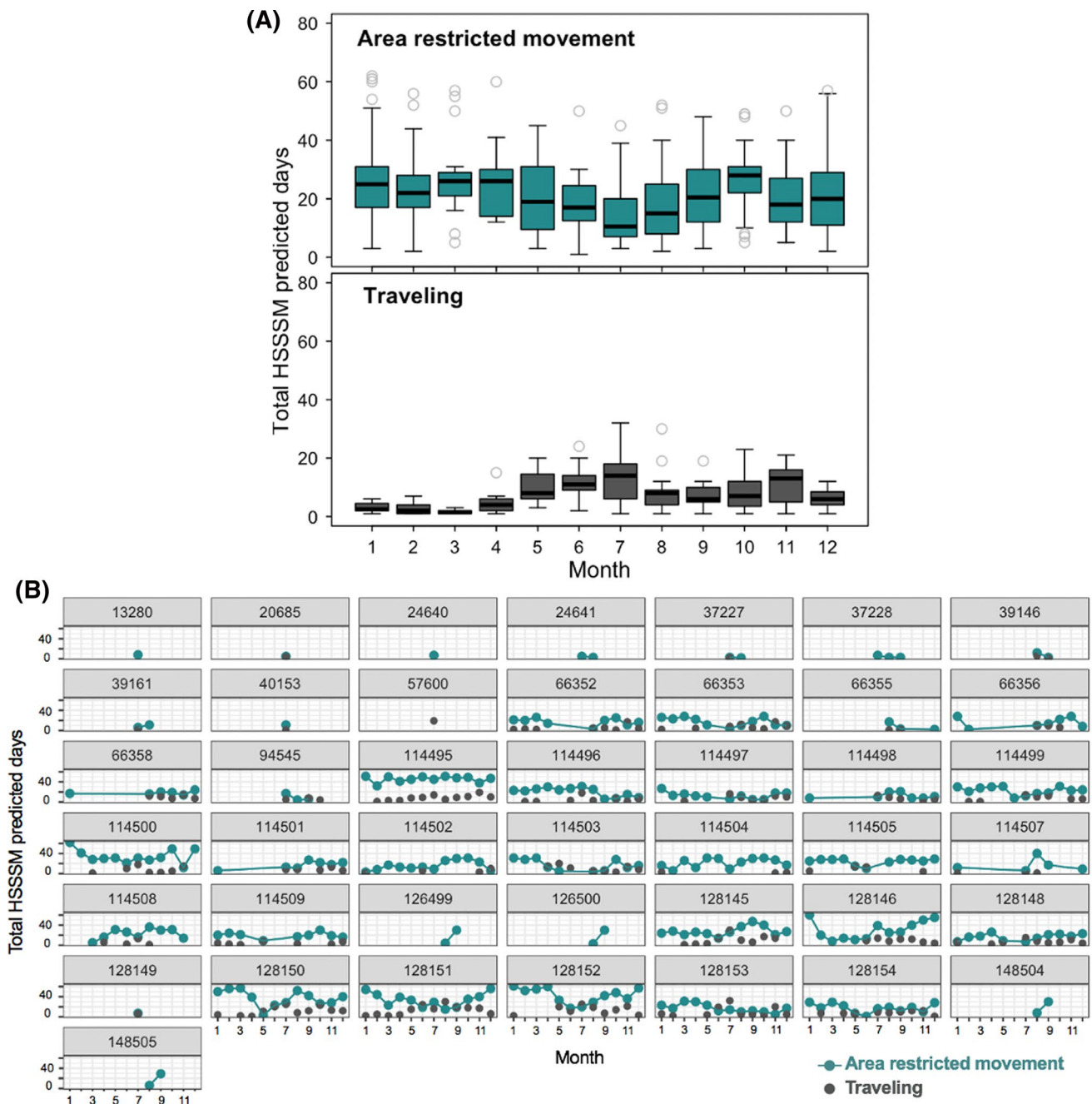
thus best describe the potential feeding areas of this age-sex group of the ECWG population.

### Factors affecting bowhead whale occupancy

When evaluating whether bowheads of different sexes and sizes allocated more or less time in particular areas (using a minimum 10 day occupancy threshold), during different seasons, we found an interaction between region and body length for the number of days spent in an area (Table 3; log-likelihood ratio test  $LRT = 16.993$ ,  $p = 0.013$ ). However, the number of days spent in an area was not affected by sex (Table 3;  $LRT = 4.523$ ,  $p = 0.104$ ) or season (Table 2;  $LRT = 1.673$ ,  $p = 0.433$ ). Furthermore, the number of days spent in a given area did not vary between different age classes of bowhead whales (Table 3;  $LRT = 2.648$ ,  $p = 0.266$ ).

We found that females were significantly larger in the Gulf of Boothia ( $13.0 \text{ m} \pm 2.12 \text{ SD}$ ,  $n = 11$ ) compared with Cumberland Sound ( $10.2 \text{ m} \pm 0.67 \text{ SD}$ ,  $n = 8$ ) using a minimum threshold of 10 days in each region during summer (Table 3;  $LRT = 8.135$ ,  $p = 0.004$ ). However, males were similarly sized in the Gulf of Boothia ( $11.3 \text{ m} \pm 1.42 \text{ SD}$ ,  $n = 11$ ) and Cumberland Sound ( $10.2 \text{ m} \pm 1.01 \text{ SD}$ ,  $n = 13$ ) (Table 3;  $LRT = 1.18$ ,  $p = 0.277$ ) (Fig. 1). The sex ratio of animals that occupied Cumberland Sound for at least 10 days in the summer were skewed towards males (64% male and





**Fig. 2** Total number of days of HSSSM predicted locations organized by month and behavioural state (Area-restricted movement and travelling). Data were pooled across years and individual ( $n=43$ ) (a) and separated by individual PTT ( $n=43$ ) (b). Only animals with > 28 Argos transmission days were included and predicted locations resulting from consecutive gaps in data exceeding 4 days were excluded.

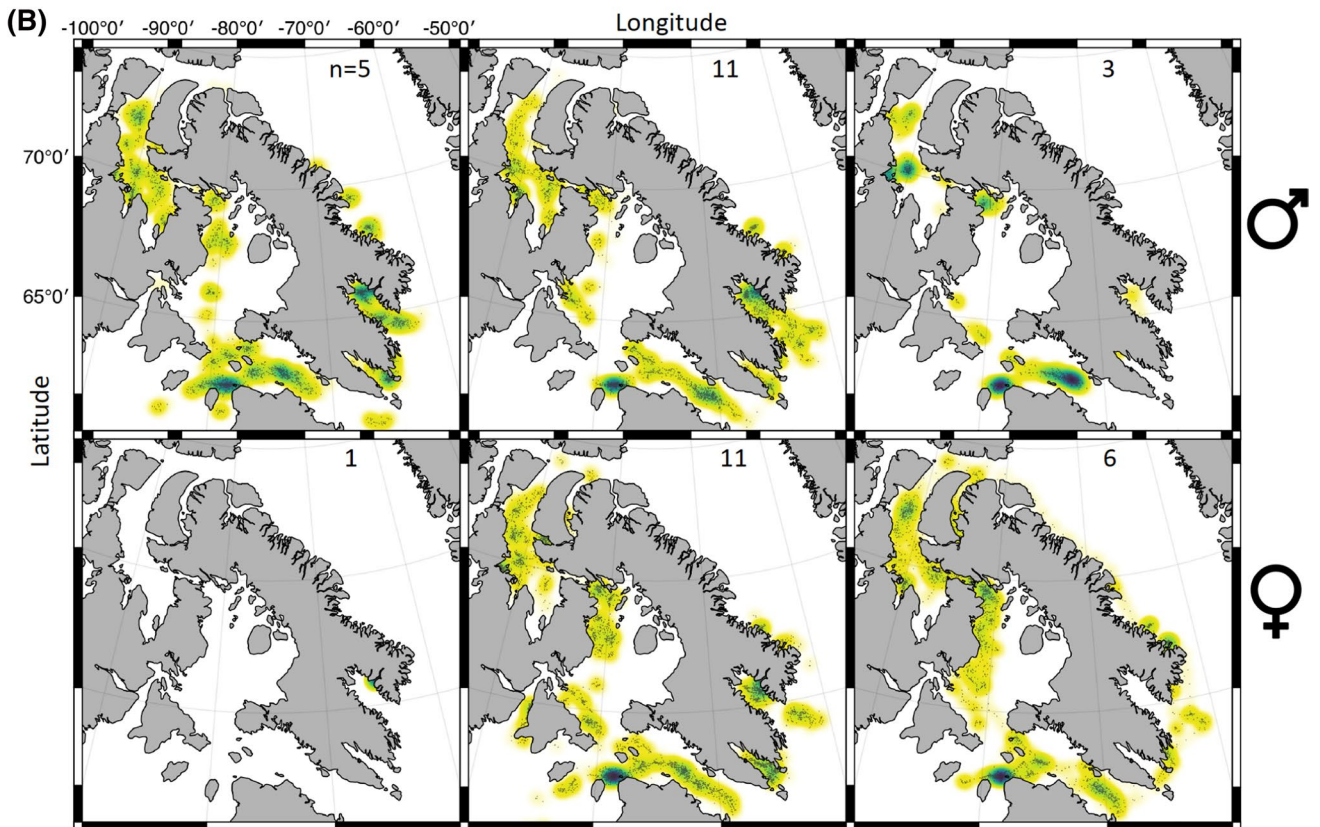
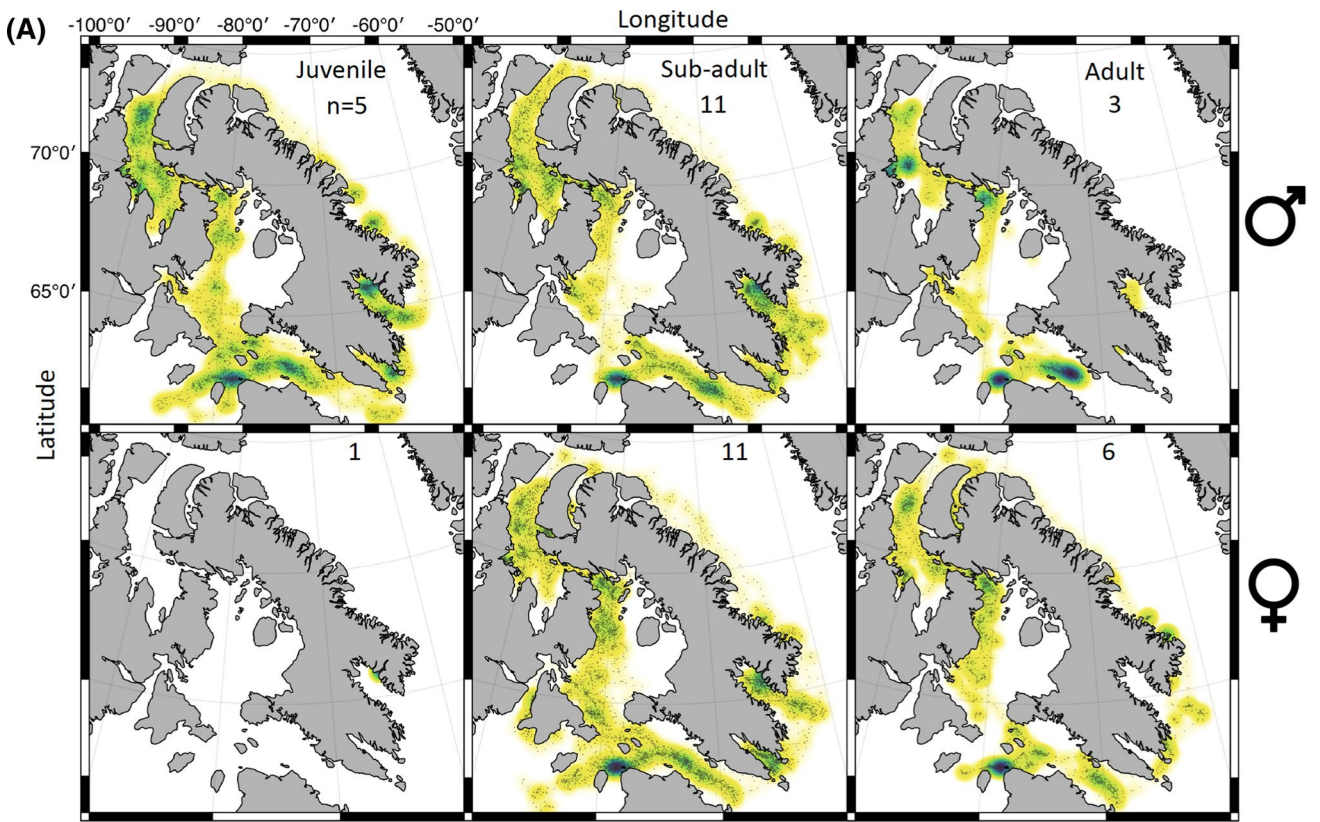
Instances where the total number of days of HSSSM predicted locations per month exceeded 30 days represent animals with long tag attachment times (> 1 year). Data include locations both inside and outside of the designated regions and thus represent the total number of days of HSSSM locations throughout their entire range

36% female;  $n=14$ ) compared with the Gulf of Boothia that had a nearly even ratio (55% male and 45% female;  $n=20$ ).

**Area use and behaviour by region**

**Cumberland Sound**

Nearly half of the tagged animals visited Cumberland Sound (48.8%;  $n=21$ ; Table 4) of all the predicted locations in





**Fig. 3** (a) All HSSSM predicted locations and (b) ARM predicted locations only for animals with >4 day consecutive gaps removed (grey circle) organized by age class and sex and a heatmap whereby yellow (yellow circle) represents areas of low density (i.e. few predicted locations), green (green circle) represents moderate density and dark blue (dark blue circle) denotes areas of high location density. Sex was determined based on genetic analysis of biopsy samples and age class was inferred based on estimated body lengths. Data are organized by juveniles (left panel), subadults (middle) and adults (right)

the Eastern Canadian Arctic ( $n = 18,294$ ), 13.7% ( $n = 2508$ ) occurred in Cumberland Sound (Fig. 3). Of these locations, 30.4% ( $n = 762$ ) belonged to females while 69.6% ( $n = 1746$ ) were from male bowhead whales. Fewer female whales ( $n = 8$ ) resided in Cumberland Sound compared with males ( $n = 13$ ). When locations were filtered by probable behavioural state, we found that travelling behaviour was associated with only 3.1% ( $n = 77$ ) of all locations in Cumberland Sound, while locations consistent with ARM behaviour represented 87.6% ( $n = 2198$ ), and 9.3% ( $n = 233$ ) were of an unknown behavioural state. These results suggest that while residing in Cumberland Sound, animals were engaged in probable foraging behaviour on a daily basis. Seasonally, the highest proportion of probable ARM locations occurred during summer 66.8% ( $n = 1469$ ), followed by spring 20.7% ( $n = 454$ ) and winter 12.51% ( $n = 275$ ).

#### East Baffin Island

Few of our tagged animals (27.9%;  $n = 12$ ; Table 4) occurred near Qikiqtarjuaq on the Eastern coast of Baffin Island as only 3.1% ( $n = 560$ ) of all predicted locations occurred in this area. The total number of predicted locations was slightly higher for females 57.3% ( $n = 321$ ) compared to males 42.7% ( $n = 239$ ). Compared with other areas, the proportion of locations associated with ARM behaviour was lower (73.8%;  $n = 413$ ) and travelling behaviour (17.5%;  $n = 98$ ) was more prevalent (unknown behavioural state 8.8%;  $n = 49$ ). Furthermore, there was strong seasonality in terms of the temporal occurrence of ARM behaviour in East Baffin Island with almost all probable foraging locations occurring during summer, 98.79% ( $n = 408$ ) and only 1.2% ( $n = 5$ ) occurring during spring and 0% in winter.

#### Hudson Strait and Frobisher Bay

Over half (58.1%,  $n = 25$ ; Table 4) of the tagged animals included locations in Hudson Strait and Frobisher Bay area-representing 23.1% ( $n = 4217$ ) of all locations in the Eastern Canadian Arctic. Of the predicted locations in this area, 46.1% ( $n = 1942$ ) were from females ( $n = 9$  individuals) and 52.7% ( $n = 224$ ) were from males ( $n = 14$  individuals). Interestingly, the locations were dominated by ARM

behaviour representing 76.9% ( $n = 3252$ ) of the total locations followed by unknown 13.6% ( $n = 574$ ) and transiting 9.3% ( $n = 391$ ). The ARM locations were highly seasonal with 57.6% ( $n = 1874$ ) during winter, 22.1% ( $n = 719$ ) during summer, and only 20.3% ( $n = 659$ ) during spring.

#### Hudson Bay

Although 41.9% ( $n = 18$ ; Table 4) of all tagged animals occurred in Hudson Bay, only 10.1% ( $n = 1840$ ) of all locations occurred within this area, suggesting both the seasonal importance of this region and that the residency period was relatively short compared with other regions. The locations were biased towards females with 53.3% ( $n = 981$ ) of the total locations ( $n = 8$  individuals) compared to males ( $n = 9$  individuals) with 45.9% ( $n = 844$ ). We found that while in Hudson Bay, the movement patterns as predicted by the HSSSM were predominately consistent with area-restricted movement and represented 78.1% ( $n = 1437$ ) of the total, compared with an unknown behavioural state consisting of 14.8% ( $n = 272$ ) and travelling including 7.1% ( $n = 131$ ). The occurrence of ARM locations was highly seasonal with 66.81% ( $n = 960$ ) occurring during spring, 28.0% ( $n = 403$ ) during winter and only 5.2% ( $n = 74$ ) during summer.

#### Gulf of Boothia

We found that 21.4% ( $n = 3915$ ) of all bowhead whale locations throughout their range occurred in the Gulf of Boothia, Prince Regent Inlet and Admiralty Inlet region (hereafter referred to as Gulf of Boothia) consisting of  $n = 25$  tagged animals (58.1% all tagged whales; Table 4). Although equal numbers of tagged males ( $n = 11$ ) and females ( $n = 11$ ) occurred in the Gulf of Boothia area, the locations were dominated by males with 54.4% ( $n = 2131$ ) compared with females 40.5% ( $n = 1586$ )—suggesting that in total, males spent more time in the Gulf of Boothia compared with females. The predicted locations consisted of 58.1% ( $n = 2275$ ) area-restricted movement locations, followed by 22.0% ( $n = 861$ ) locations of unknown behavioural state and 20.0% ( $n = 779$ ) travelling locations. As a high-latitude region, we found considerable seasonality in terms of the number of ARM-associated locations with no locations during winter and spring and 100% ( $n = 2275$ ) of all ARM locations during summer. The seasonality of probable foraging behaviour is likely a function of the seasonal timing of the ice breakup in the area (Ferguson et al. 2010).

#### Lancaster Sound

Although 30.2% ( $n = 13$ ; Table 4) of tagged whales occurred in Lancaster Sound, we found that the smallest proportion 0.84% ( $n = 154$ ) of locations occurred in this

**Table 3** Linear mixed-effects models for the impacts of habitat, season, body length, sex, and age class on the number of days spent in an area

Model	Fixed	df	AIC	LR test	$\Delta$ AIC
<i>Number of days (all regions)</i>					
Null	~ 1	94	333.110	~	~
1	~ Region	88	319.694	25.416 (p=0.000)	13.416
2	~ Region + age.class	88, 36	321.047	2.648 (p=0.266)	- 1.353
3	~ Region + length	88, 37	315.180	6.514 (p=0.011)	4.514
4	~ Region $\times$ length	82, 37	308.755	18.425 (p=0.005)	6.425
5	~ Region $\times$ length + sex	82,35,35	308.559	4.196 (p=0.123)	0.197
6	~ Region *length + season	80,37,80	307.720	5.036 (p=0.081)	0.281
<i>Female body length (GB &amp; CS)</i>					
7	~ 1	14	- 124.8945	~	~
8	~ Region	12	- 131.0299	8.135 (p=0.004)	- 6.1354
<i>Male body length (GB &amp; CS)</i>					
9	~ 1	17	- 383.4093	~	~
10	~ Region	6	- 382.5931	1.184 (p=0.277)	0.8162

We compared residuals of two models—one with a natural logarithm (ln) transformed and another with an untransformed dependent variable (number of days spent in an area). We found that the untransformed model had residuals that were not perfectly normally distributed as some variation or curvature existed compared with the transformed model. Consequently, all models used the ln transformation of the number of days spent in an area. The change in AIC ( $\Delta$  AIC) and likelihood ratio tests (LRT) are relative to the model earlier in the list for the number of days, with the exception of model 6, which we compared with model 3 and these indicate that there are interactions between region and body length for the number of days an animal occupied a specific area. However, we found no support for models that incorporated sex, age class, and seasonal effects (models 2, 5 & 6). Nor did we find evidence that male body length varied between Gulf of Boothia and Cumberland Sound (model 10)

region. The sex ratio of predicted locations from tagged animals in Lancaster Sound was slightly skewed towards females ( $n = 6$  individuals) with 56.5% ( $n = 87$ ) compared with 43.0% ( $n = 66$ ) males ( $n = 6$  individuals). Unlike other regions, travelling accounted for the greatest proportion of all predicted locations with 50.6% ( $n = 78$ ) compared with ARM locations accounting for only 34.4% ( $n = 53$ ) and 15.0% ( $n = 23$ ) for unknown. We only found ARM-associated locations during summer (100%;  $n = 53$  of all locations in this area).

### Foxe Basin

The highest proportion of tagged animals 74.4% ( $n = 32$ ; Table 4) occurred in Foxe Basin where 13.4% ( $n = 2443$ ) of the predicted locations were also found. Overall, a greater proportion of locations came from tagged females ( $n = 16$  individuals) 57.8% ( $n = 1413$ ) than males ( $n = 14$  individuals) 37.2% ( $n = 908$ ). Furthermore, we found that the locations were dominated by ARM (52.0%,  $n = 1271$ ), followed by travelling (28.7%,  $n = 702$ ) and an unknown behavioural state (19.2%,  $n = 470$ ). Similar to the Gulf of Boothia area, locations associated with ARM were highly seasonal in Foxe Basin where 97.7% ( $n = 1242$ ) of ARM locations occurred during summer, 2.20% ( $n = 28$ ) in spring and 0.08% ( $n = 1$ ) during winter.

### Sex-specific foraging behaviour

Overall, we found that 15,637 predicted locations ( $n = 43$  tagged animals) occurred within specific regions (Fig. 1; Table 5), representing the movements of slightly more females ( $n = 21$ ) than males ( $n = 19$ ) and only 3 whales of unknown sex. Area-restricted movement represented 68.7% ( $n = 10,899$ ) of all predicted locations with travelling behaviour representing only 14.4% ( $n = 2256$ ) and an unknown behavioural state accounting for 15.9% ( $n = 2482$ ). When examining the latitudinal and longitudinal ARM-associated locations of male and female bowhead whales between 2012 and 2015 (when tag attachments were longest) we found seasonal patterns whereby animals occurred at comparatively higher latitudes during summer and at lower latitudes during winter (Fig. 4). This shift in distribution matched what was expected based on the seasonal timing of sea ice formation and retreat in the Eastern Canadian Arctic.

Through comparison of the percent of all predicted locations by behavioural state and across regions, we found that the greatest number of locations occurred in the Gulf of Boothia and Hudson Strait (Fig. 5; Table 5)—suggesting that the residency period was highest in these two areas. For example, Gulf of Boothia accounted for 21.0% of all region-specific ARM locations and Hudson Strait comprised 29.8%. When accounting for sex, the Gulf of Boothia, Foxe Basin and Hudson Strait contained the greatest proportion of all

**Table 4** Total number of SPLASH tagged whales (# Animals) with HSSSM predicted locations excluding >4 consecutive days of gaps in data, organized by region, season and probable behaviour with data pooled across years

Region	Season	Behaviour	# Animals
Cumberland Sound	Summer	ARM	17
Cumberland Sound	Summer	Travelling	10
Cumberland Sound	Summer	Unknown	11
Cumberland Sound	Winter	ARM	6
Cumberland Sound	Winter	Travelling	2
Cumberland Sound	Winter	Unknown	4
Cumberland Sound	Spring	ARM	8
Cumberland Sound	Spring	Travelling	6
Cumberland Sound	Spring	Unknown	7
		Total	21
East Baffin Island	Summer	ARM	10
East Baffin Island	Summer	Travelling	11
East Baffin Island	Summer	Unknown	9
East Baffin Island	Spring	ARM	1
East Baffin Island	Spring	Travelling	1
East Baffin Island	Spring	Unknown	1
		Total	12
Foxe Basin	Summer	ARM	25
Foxe Basin	Summer	Travelling	26
Foxe Basin	Summer	Unknown	28
Foxe Basin	Winter	ARM	1
Foxe Basin	Winter	Unknown	1
Foxe Basin	Spring	ARM	3
Foxe Basin	Spring	Travelling	7
Foxe Basin	Spring	Unknown	5
		Total	32
Gulf of Boothia	Summer	ARM	23
Gulf of Boothia	Summer	Travelling	24
Gulf of Boothia	Summer	Unknown	23
		Total	25
Hudson Bay	Summer	ARM	6
Hudson Bay	Summer	Travelling	5
Hudson Bay	Summer	Unknown	7
Hudson Bay	Winter	ARM	13
Hudson Bay	Winter	Travelling	1
Hudson Bay	Winter	Unknown	4
Hudson Bay	Spring	ARM	17
Hudson Bay	Spring	Travelling	9
Hudson Bay	Spring	Unknown	11
		Total	18
Hudson Strait	Summer	ARM	20
Hudson Strait	Summer	Travelling	20
Hudson Strait	Summer	Unknown	18
Hudson Strait	Winter	ARM	20
Hudson Strait	Winter	Travelling	16
Hudson Strait	Winter	Unknown	18
Hudson Strait	Spring	ARM	16

**Table 4** (continued)

Region	Season	Behaviour	# Animals
Hudson Strait	Spring	Travelling	10
Hudson Strait	Spring	Unknown	12
Hudson Strait	Summer	ARM	6
		Total	25
Lancaster Sound	Summer	Travelling	11
Lancaster Sound	Summer	Unknown	4
		Total	13

Total is the number of unique individuals that visited each region

predicted female locations and that ARM was most prevalent in Gulf of Boothia (9.2%;  $n = 1001$ ), Foxe Basin (6.8%;  $n = 741$ ), Hudson Strait (13.8%;  $n = 1506$ ) (Fig. 5) suggested that these are important areas for females to seasonally forage. For males, however, Hudson Strait accounted for 15.7% ( $n = 1714$ ) of all ARM locations but that Cumberland Sound represented 14.1% ( $n = 1542$ ) followed by Gulf of Boothia with 10.7% ( $n = 1162$ ) of ARM locations.

## Discussion

The observed seasonal patterns in area-restricted movement and traveling behaviour are consistent with previous descriptions of bowhead whale migratory movement in the Eastern Canadian Arctic, whereby animals make northward movements during the spring and summer when sea ice coverage is lowest (Reeves and Heide-Jørgensen 1996; Cosens and Innes 2000; Cosens and Blouw 2003; Heide-Jørgensen et al. 2010; Higdon and Ferguson 2010; Nielsen et al. 2015) to forage in high-latitude regions and then when sea ice begins to reform, migrate south during the fall to overwinter predominately in Hudson Strait (Heide-Jørgensen et al. 2003; Laidre et al. 2007; Ferguson et al. 2010; Pomerleau et al. 2011a). Consequently, we would expect that individuals would exhibit horizontal movement consistent with area-restricted search most often during winter when movements are restricted by the presence of sea ice. Conversely, traveling movements would be most prevalent during summer as animals expand their range to seasonally ice-covered areas, such as Prince Regent Inlet, Gulf of Boothia, Admiralty Inlet and Lancaster Sound (Fig. 6).

Northbound summer migrations coincide with the timing of the phytoplankton blooms at or underneath the ice edge (Fortier et al. 2002; Mundy et al. 2009, 2014; Arrigo et al. 2012) and in open water following seasonal ice melt (Kahru et al. 2016) between April and June (Reeves and Mitchell 1990; Madsen et al. 2001; Swalethorp et al. 2011; Fujiwara et al. 2016) that occurs after the ice breakup and results in the ascension of diapausing calanoid copepods such as

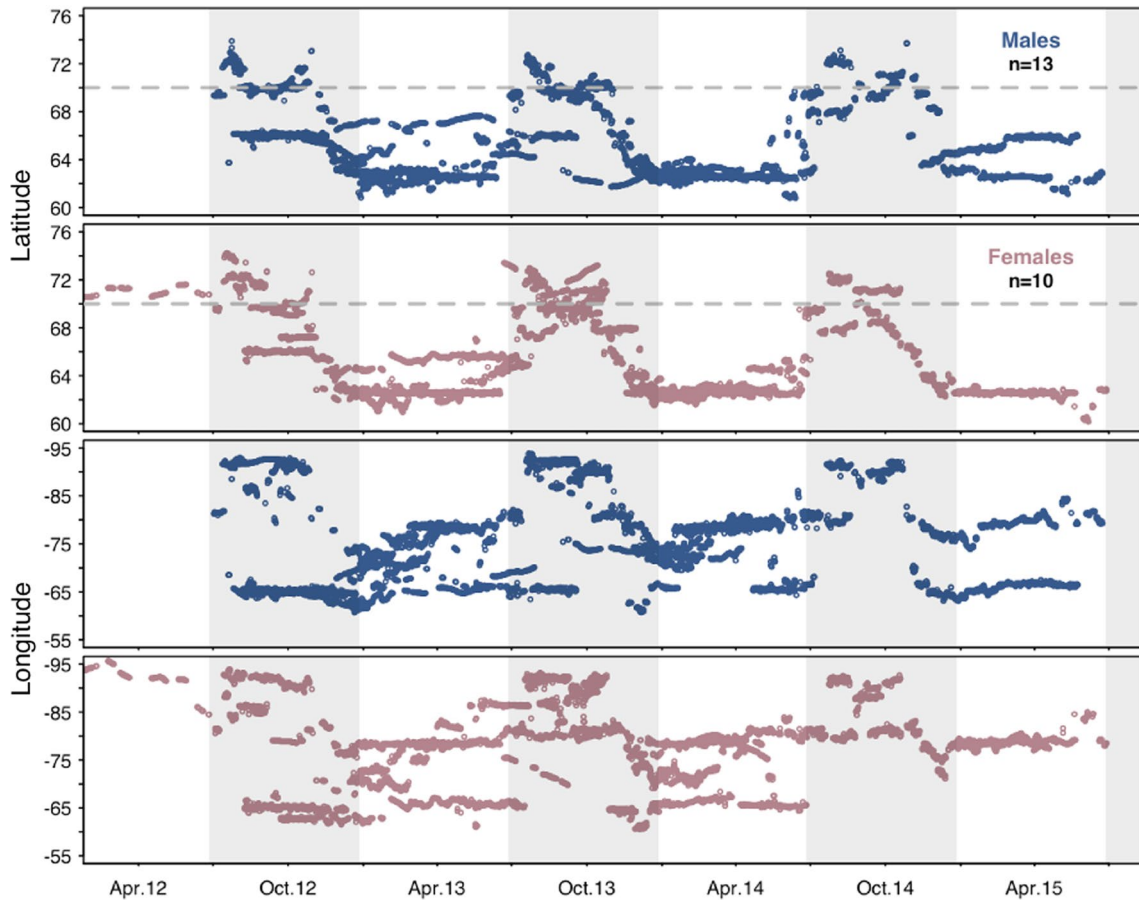
**Table 5** Percent of total predicted locations (% total) by behavioural state (behaviour) and sex that occurred in each identified region (region)

Region	Locations ( <i>n</i> )	% Total	Behaviour	Sex
Cumberland Sound	656	6.0	ARM	Female
East Baffin Island	242	1.2	ARM	Female
Foxe Basin	741	6.8	ARM	Female
Gulf of Boothia	1001	9.2	ARM	Female
Hudson Bay	728	6.7	ARM	Female
Hudson Strait and Frobisher Bay	1506	13.8	ARM	Female
Lancaster Sound	49	0.4	ARM	Female
Cumberland Sound	24	1.1	Travelling	Female
East Baffin Island	54	2.4	Travelling	Female
Foxe Basin	354	15.7	Travelling	Female
Gulf of Boothia	280	12.4	Travelling	Female
Hudson Bay	83	3.7	Travelling	Female
Hudson Strait and Frobisher Bay	125	5.4	Travelling	Female
Lancaster Sound	31	1.4	Travelling	Female
Cumberland Sound	82	3.3	Unknown	Female
East Baffin Island	25	1.0	Unknown	Female
Foxe Basin	318	12.8	Unknown	Female
Gulf of Boothia	305	12.3	Unknown	Female
Hudson Bay	170	6.8	Unknown	Female
Hudson Strait and Frobisher Bay	311	12.5	Unknown	Female
Lancaster Sound	7	0.3	Unknown	Female
Cumberland Sound	1542	14.1	ARM	Male
East Baffin Island	171	1.7	ARM	Male
Foxe Basin	439	4.2	ARM	Male
Gulf of Boothia	1162	10.7	ARM	Male
Hudson Bay	694	6.4	ARM	Male
Hudson Strait and Frobisher Bay	1714	15.7	ARM	Male
Lancaster Sound	3	0.0	ARM	Male
Cumberland Sound	53	2.3	Travelling	Male
East Baffin Island	44	2.0	Travelling	Male
Foxe Basin	328	14.5	Travelling	Male
Gulf of Boothia	457	20.3	Travelling	Male
Hudson Bay	48	2.1	Travelling	Male
Hudson Strait and Frobisher Bay	257	11.4	Travelling	Male
Lancaster Sound	47	2.1	Travelling	Male
Cumberland Sound	151	6.1	Unknown	Male
East Baffin Island	24	1.0	Unknown	Male
Foxe Basin	141	5.7	Unknown	Male
Gulf of Boothia	512	20.6	Unknown	Male
Hudson Bay	102	4.1	Unknown	Male
Hudson Strait and Frobisher Bay	253	10.2	Unknown	Male
Lancaster Sound	16	0.6	Unknown	Male
Foxe Basin	91	0.8	ARM	Unknown
Gulf of Boothia	112	1.0	ARM	Unknown
Hudson Bay	15	0.1	ARM	Unknown
Hudson Strait and Frobisher Bay	32	0.3	ARM	Unknown
Lancaster Sound	1	0.0	ARM	Unknown
Foxe Basin	20	0.9	Travelling	Unknown
Gulf of Boothia	42	1.9	Travelling	Unknown
Hudson Strait and Frobisher Bay	9	0.4	Travelling	Unknown
Foxe Basin	11	0.4	Unknown	Unknown



**Table 5** (continued)

Region	Locations (n)	% Total	Behaviour	Sex
Gulf of Boothia	44	1.8	Unknown	Unknown
Hudson Strait and Frobisher Bay	10	0.4	Unknown	Unknown



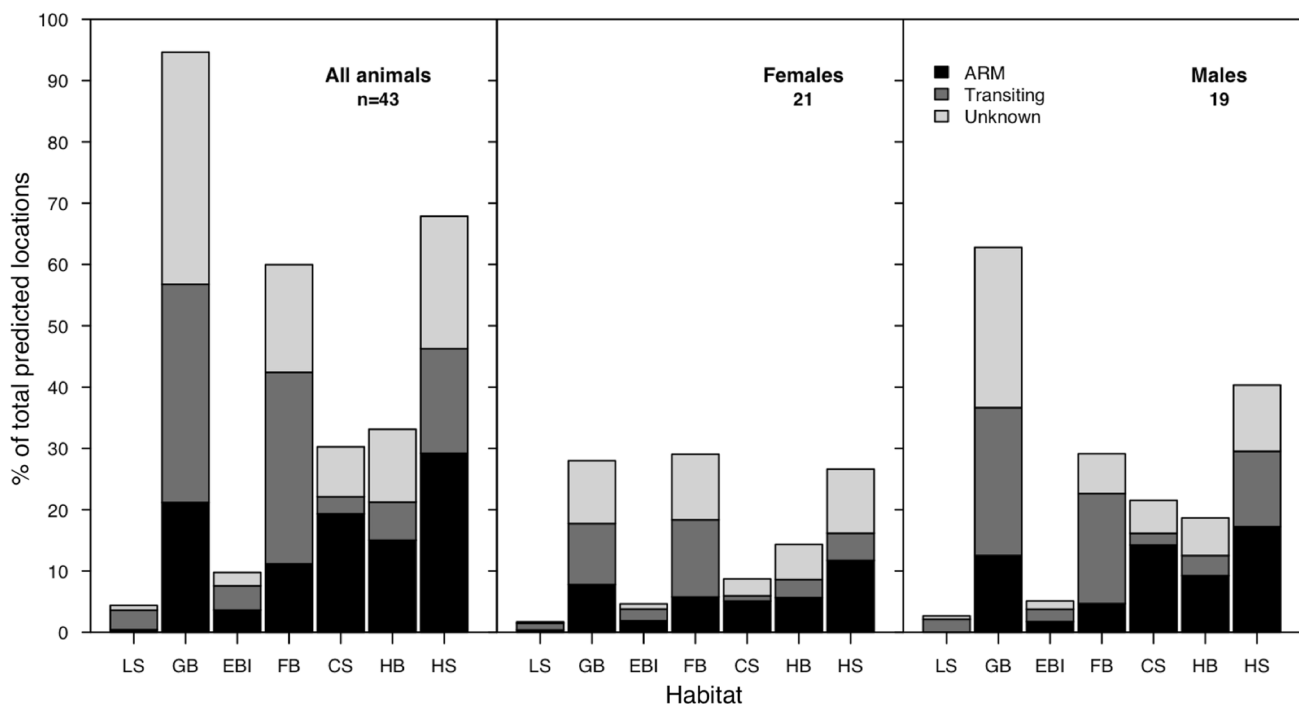
**Fig. 4** Latitudes (top panels) and longitudes (bottom) of predicted locations between spring 2012 and winter 2015 when the longest tag attachments occurred on animals providing improved resolution to examine seasonal fluctuations in habitat use. Plotted are locations associated with area-restricted movement behaviour for males (blue

circles) and females (pink circles). The shaded areas represent summer as occurring between 27 June and 27 December. The horizontal reference line (70° latitude; dotted lines) highlights locations at higher latitudes during summer

*Calanus glacialis* and *Calanus hyperboreus* (Falk-Petersen et al. 2009). Bowhead whales have also been observed to feed on *Calanus* spp. before they have ascended to surface waters to feed on phytoplankton (Nielsen et al. 2015; Fortune 2018). Consequently, the whales are likely responding to latitudinal differences in the timing of phytoplankton blooms and *Calanus* spp. ascension.

The lack of support for linear mixed-effects models testing for differences in habitat use by sex and age class was somewhat counter to our expectation because previous studies using genetic analysis of biopsy samples, found evidence of sexual segregation across habitats for ECWG bowhead whales (Heide-Jørgensen et al. 2010). However, since our

sample sizes were inherently smaller ( $n = 43$  tagged animals) than the Heide-Jørgensen et al. (2010) study ( $n = 806$  biopsy samples) and because our tagged animals were predominately from one age class (i.e. subadults), we may not have had sufficient power to detect a significant difference between age classes. However, body size is a function of age such that older animals are larger (George et al. 1999) and thus habitat selection may in part be a function of energetics, whereby larger, older animals require a greater total daily biomass of prey compared to smaller and younger individuals and occupy more northern areas where zooplankton species composition and biomass are presumably dominated by large bodied, Arctic taxa (e.g. *Calanus hyperboreus*)



**Fig. 5** Percent of all predicted HSSSM locations by behavioural state (area-restricted movement, travelling and unknown) and habitat as well as the percent of all predicted locations by behavioural state that were from tagged females, males organized by habitat (LS Lancaster

Sound, GB Gulf of Boothia, EBI East Baffin Island, FB Foxe Basin, CS Cumberland Sound, HB Hudson Bay, HS Hudson Strait). Sample sizes are the number of tagged animals

compared with more southern areas that contain a higher proportion of smaller bodied, temperate species (e.g. *Calanus finmarchicus*) (Pomerleau et al. 2011b). Furthermore, larger animals may be less susceptible to predation from killer whales and this may result in increased habitat flexibility.

## Area use and behaviour by region

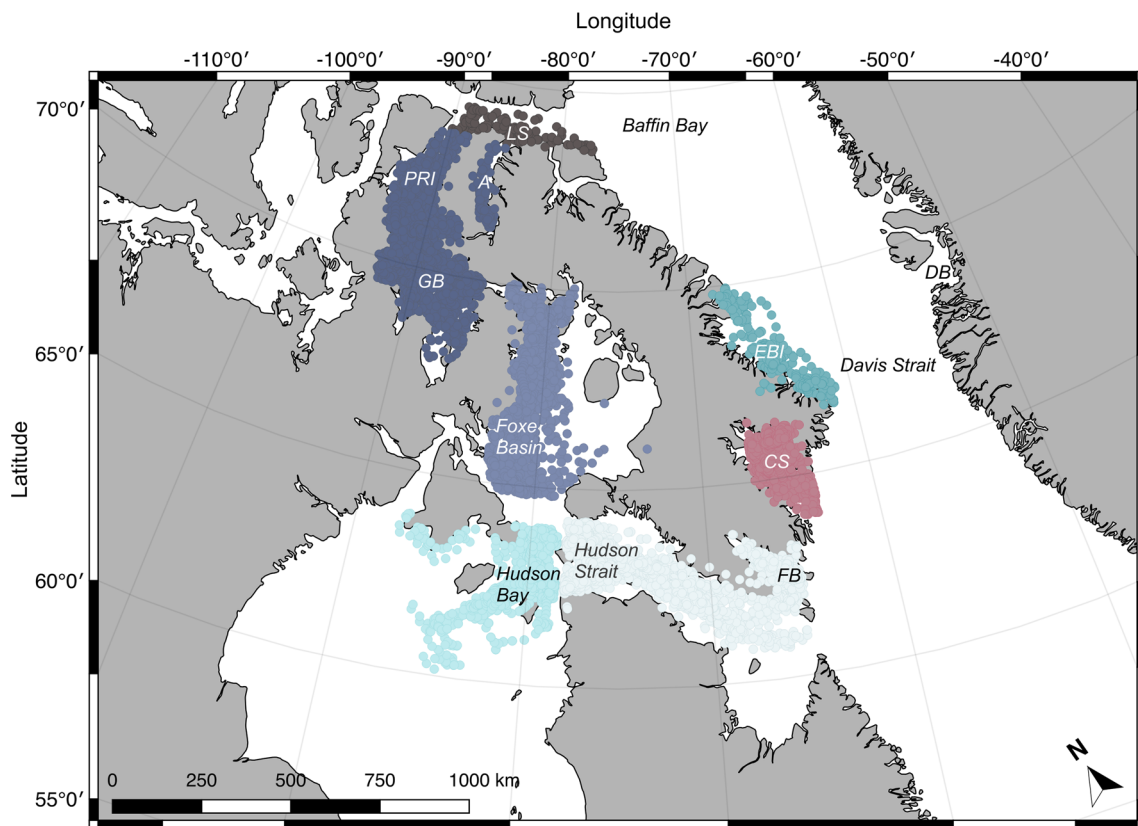
### Cumberland Sound

Area selection may also represent strategies to minimize killer whale predation risk (Ford and Reeves 2008) such that ~10% of the documented ECWG population bore scars from killer whale attacks (Reinhart et al. 2013) and larger animals occupy more northern regions where they may be more likely to encounter killer whales (Higdon et al. 2012). Additionally, we found that females occupying high-latitude habitats were larger on average (13 m) in body length than females in Cumberland Sound (10 m) which is a lower-latitude habitat. However, we did not find similar patterns in body size for males as animals in the Gulf of Boothia (11 m) were not significantly larger than those in Cumberland Sound (10 m), suggesting that body size is not a good predictor for habitat use for juvenile and subadult males. The fact that we found proportionally more males

in lower-latitude habitats such as the Cumberland Sound suggests that perhaps this area is preferred by juvenile and subadult males. In fact, other studies have also documented a somewhat skewed sex ratio in Cumberland Sound (45% female) providing further support that this habitat disproportionately supports feeding activities of younger, male whales (Heide-Jørgensen et al. 2010; Frasier et al. 2020).

### East coast of Baffin Island

It appears as though the east coast of Baffin Island is not a common foraging area for the subadult Eastern Canada-West Greenland bowhead whales and that it is most frequented during late summer. When examining all predicted locations, it is apparent that the majority of locations along the Eastern coast of Baffin Island are associated with travelling behaviour (Fig. 3) and thus it appears that subadult animals utilize this shoreline principally for migratory purposes. Our results contrast with other satellite telemetry studies (Kjellerup et al. 2015; Nielsen et al. 2015), which found evidence of adult bowhead whale foraging behaviour based on dive rates and horizontal movement, along the Eastern shore of Baffin Island in Clyde Inlet and Isabella Bay. The apparent differences in results are likely attributed to differences in demographic composition of tagged animals in both studies (e.g. adult animals originating from Disko Bay;



**Fig. 6** Predicted locations ( $n=43$  animals) for all behavioural states separated by region, whereby Prince Regent Inlet (PRI), Gulf of Boothia (GB) and Admiralty Inlet (AI) are treated as one area and Hudson Strait and Frobisher Bay (FB) are similarly considered to be the same area due to latitudinal similarity. Furthermore, DB represents Disko Bay and CS denotes Cumberland Sound. Latitude and

longitude (decimal degrees) criteria used to filter predicted locations by habitat areas in the Eastern Canadian Arctic, whereby locations that were greater than the minimum latitude, less than the maximum latitude, greater than the minimum longitude and less than the maximum longitude were assigned to a particular habitat (Table 2)

Nielsen et al. 2015 and predominately subadults from Foxe Basin and Cumberland Sound). Consequently, these divergent results suggest that East Baffin Island may be preferentially utilized for foraging by non-lactating adult females that inhabit Disko Bay in late winter–early spring compared with subadult and adult animals originating from Foxe Basin and Cumberland Sound in summer.

#### Hudson Strait and Frobisher Bay

The high proportion of ARM-associated locations in Hudson Strait and Frobisher Bay suggests that the whales engaged in foraging related activities on a daily basis including during winter (Matthews and Ferguson 2015; Pomerleau et al. 2018). However, the propensity of ARM-associated locations—specifically during winter, may also be partially attributed to the small area of open water in Hudson Strait during the winter and thus the daily movements of animals may be restricted while occupying this region.

#### Hudson Bay

It appears as though foraging activities are predominately occurring during the spring and this may be a function of the earlier breakup of sea ice in Hudson Bay compared with more northern regions and the presumably earlier phytoplankton bloom (Ferland et al. 2011; Assmy et al. 2017) and vertical aggregation of calanoid copepods (Rochet and Grainger 2009). Studies examining the spatial distribution and species composition of zooplankton in Hudson Bay found low abundances of Calanoid copepods, which are the preferred prey of bowhead whales, during September and this may help explain why the tagged whales were nearly absent from this region during summer (Harvey et al. 2001).

#### Lancaster Sound

The low residency of tagged bowhead whales in Lancaster Sound was somewhat surprising as other studies (e.g. Nielsen et al. 2015; Chambault et al. 2018) found that adult

females originally tagged in late winter–early spring, utilized Lancaster Sound during summertime. The apparent differences between our satellite telemetry studies may in part reflect sample biases where our study included predominately subadult animals tagged in Canada while the other studies (Nielsen et al. 2015; Chambault et al. 2018) focused on movement and area-use patterns of mostly tagged adult females originating from Disko Bay (Greenland) as they represent 78% of the local population (Heide-Jørgensen et al. 2010). Our tagged females were  $12.3 \text{ m} \pm 1.19$  ( $n=6$ ) SD long (range 11.0 to 13.5 m) and were mostly probable subadults with one probable adult female. The males in our study were smaller than the tagged females and measured  $10.4 \text{ m} \pm 1.38$  SD ( $n=6$ ) (range 9.0–12.0 m) and thus included juveniles and subadult animals. It is interesting, that even though a probable adult female (PTT 114499; median body length was 13.5 m) was in Lancaster Sound, she only had a short residency of at least 16.5 days. This female was tagged in Foxe Basin in 2012 and spent 1.5 days in the same area post-tagging and then resided in the Gulf of Boothia for a minimum of 38.5 days between 8 July and 3 September. Consequently, it appears as though, in our study, the Gulf of Boothia was preferred over Lancaster Sound for foraging activities.

### Foxe Basin

Compared with the other regions frequented by ECWG bowhead whales, the proportion of travelling locations were high in Foxe Basin and may suggest that this area is used partially as a migratory route from winter habitat to the Gulf of Boothia, Prince Regent Inlet, Admiralty Inlet and Lancaster Sound through Fury and Hecla Strait to permit high-latitude foraging during mid-summer. The whales appear to only use the western side of Foxe Basin (Figs. 3, 4), which is known to be deeper and contain higher proportions of calanoid copepods than the warmer and shallower Eastern portion of Foxe Basin (Grainger 1962). Consequently, it seems reasonable that while migrating to higher-latitude feeding areas, the animals take advantage of opportunistic feeding opportunities in Foxe Basin.

### Gulf of Boothia

Our analysis of long-term satellite telemetry data revealed that the Gulf of Boothia, Prince Regent Inlet and Admiralty Inlet are important summertime areas for bowhead whales as over half of the tagged whales visited this region. However, no tagged whales originating from Disko Bay occupied Admiralty Inlet and few resided in Gulf of Boothia and Prince Regent Inlet (Nielsen et al. 2015). Instead, animals from Disko Bay utilized areas on the Eastern coast of Baffin Island such as Clyde Inlet and Isabella Bay (Nielsen et al.

2015)—areas that were infrequently used by our tagged whales.

Although the mechanism responsible for divergent patterns in habitat use for bowheads originating in Disko Bay vs. Foxe Basin and Cumberland Sound is unknown, it may relate to geographical accessibility and predation risk. In both cases, habitat selection may be driven by energetics such that animals are minimizing the distanced travelled to access productive summertime feeding habitats and maximize their net energy gain (Braithwaite et al. 2015). Since killer whales are likely more successful at hunting smaller and younger bowheads (Reinhart et al. 2013), it is also possible that less time spent travelling may also reduce exposure to predators—particularly for the juvenile and subadult animals originating from Foxe Basin and Cumberland Sound (Corkeron and Connor 1999; Matthews et al. 2011, 2020). Although a higher proportion of larger bodied, females occupy the Gulf of Boothia region compared with Cumberland Sound, smaller bodied juveniles and subadult animals also frequent this area. Bowheads employ a fight strategy (Ford and Reeves 2008) in response to predatory attack and are known to occupy shallow coastal waters and hide under sea ice (Mitchell and Reeves 1982; Reeves and Mitchell 1988; Finley 2001; Shpak and Paramonov 2018), which has been well documented by Inuit (Finley 1990; NWMB 2000; Ferguson et al. 2012). Consequently, the persistence of ice in the Gulf of Boothia during summer may permit more vulnerable age classes (e.g. juveniles) of bowheads (Young et al. 2019) to utilize this area by providing predator refuge from mammal-eating killer whales (Matthews et al. 2020). Conversely, non-lactating adult female bowheads originating from Disko Bay may be less susceptible to killer whale attack and thus their habitat selection may be less affected by predator avoidance.

### Sex-specific foraging behaviour

Like other Arctic cetacean species, different regions within the Eastern Canadian Arctic appear to be of greater importance to particular age–sex groups of bowhead whales. Both narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*) commonly cluster in groups based on size, age and reproductive status (Marcoux et al. 2009; Asselin et al. 2012; Colbeck et al. 2013; Charry et al. 2020) and this translates into differences in the composition and trophic level of consumed prey (Loseto et al. 2008; Marcoux et al. 2012). Although the total number of HSSM locations in the Gulf of Boothia is greater for males, females proportionally spend more time in the Gulf of Boothia than other regions compared with males—suggesting this region is particularly important for adult females and females approaching sexual maturity during summertime. A common migratory route to the Gulf of Boothia was through the western portion



of Foxe Basin, which is also an area where predominately female bowheads were found. Unlike larger, female bowheads that appear to preferentially occupy higher-latitude summer regions (i.e. Gulf of Boothia, Prince Regent Inlet and Admiralty Inlet), male bowheads show a slight preference for lower-latitude summering grounds such as Cumberland Sound for probable foraging activities. Conversely, it appears as though Hudson Strait is an equally important area for both male and female bowheads during the winter when annual sea ice is at its maximum extent and thickness—presumably to feed on diapausing calanoid copepods.

Our findings shed light on the long-term, seasonal movements, behaviour and area-use patterns of different age–sex groups of bowhead whales in the Eastern Canadian Arctic. We found that the north/south movements of bowhead whales although masked by the predominance of large islands (e.g. Baffin) were considerably seasonal and matched what was expected given the latitudinal timing of sea ice melt and formation. Furthermore, we found that male and female bowhead whales occupied similar areas (with the exception of Gulf of Boothia and Cumberland Sound) and that Lancaster Sound was not an important area for at least a subset of the ECWG bowhead whale population—consisting of predominately subadults. We found evidence of Foxe Basin serving more as a corridor than a foraging ground during summer based on the prevalence of predicted locations associated in travelling behaviour. Furthermore, we found that during summer, whales tended to select either Cumberland Sound or Gulf of Boothia region for probable foraging and that a higher proportion of males utilized Cumberland Sound compared with the Gulf of Boothia. The apparent differences in area selection may in part be a function of predator avoidance, whereby smaller, juvenile males may select Cumberland Sound over higher-latitude regions where they may be more likely to encounter killer whales during their travels (Higdon et al. 2012; Breed et al. 2017). Alternatively, dissimilarities in habitat selection may reflect differences in energetic requirements and animals ability to meet their daily food needs such that subadult females likely have higher total daily energy needs due to their larger size and thus require higher abundances or better quality prey than their smaller, male counterparts (Laidre et al. 2007; George 2009). However, determining what biological mechanism is ultimately driving the apparent size differences in area selection requires knowing (1) how the quality and quantity of prey available to bowhead whales differs between the Gulf of Boothia and Cumberland Sound and (2) how the occurrence of killer whales and attempted bowhead whale predation (Young et al. 2019) rates vary between the two regions.

It is uncertain how bowhead whale movements will change in response to continued sea ice loss (Notz and Stroeve 2016; Stroeve et al. 2017), greater prevalence of competitors (e.g. temperate zooplanktivorous predators;

Higdon and Ferguson 2011; Brower et al. 2018) and predators (Finley 1990; Matthews et al. 2011; Young et al. 2011; Higdon et al. 2012; Reinhart et al. 2013). It may be that the timing of the northern migration occurs earlier over time and that animals expand their northern summer range into the high Arctic Archipelago as primary production increases into areas historically dominated by multiyear ice (Dyke and England 2003; Renaut et al. 2018). Good feeding habitat that occurs close to the ice edge and affords protection from killer whale predation may change in the near future. For example, intraspecific competition for resources may increase in high-latitude feeding grounds such as the Gulf of Boothia as males may allocate proportionally less time to feeding in southern regions such as Cumberland Sound that are likely to experience climate-induced changes in prey quality and quantity sooner than more northern areas. Furthermore, animals may begin taking advantage of secondary phytoplankton blooms that facilitate the aggregation of copepods near the surface at lower latitudes (Fujiwara et al. 2016). Consequently, the habitat-use patterns and foraging season of bowhead whales are likely to change in location and duration in the future. However, the population level responses to climate change are unknown as we need to determine how the quality and quantity of prey may shift overtime.

**Acknowledgements** We are most appreciative of the support provided by our project partners, Levi Qaunaq and Natalino Piugattak from Igloodik, and Noah Ishulutaq and Timeosie Akpallialuk from Pangnirtung for vessel operations and Bernard LeBlanc for tagging and biopsy collection. We are grateful for the invaluable logistical support provided by the Igloodik and the Pangnirtung Hunters and Trappers Organization. Fieldwork was funded by Fisheries and Oceans Canada, Nunavut Wildlife Research Trust Fund, Nunavut General Monitoring Program, Ocean Tracking Network, University of Manitoba, ArcticNet Centre of Excellence awarded to S.H. Ferguson. This manuscript was improved thanks to the helpful recommendations of William Koski and two anonymous reviewers.

## Compliance with ethical standards

**Conflict of interest** There are no conflicts of interest to declare.

**Ethical approval** The tagging procedures were approved by DFO Freshwater Institute Animal Care Committee (AUP # FWI-ACC-2002, 2003, 2004, 2005, 2006 and 2007) and under DFO License to Fish for Scientific Purposes #S-02/03 to 05/06-1019-NU and #S-12/13-1024-NU, S-13/14-1009-NU and S-16/17 1005-NU.

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