



Bowhead whale *Balaena mysticetus* seasonal selection of sea ice

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ABSTRACT: Highly mobile large-bodied organisms are adapted to seasonal variation associated with polar environments. We used satellite tracking data from 27 bowhead whales *Balaena mysticetus* of the Eastern Canada-West Greenland population to test for movement and habitat selection of the highly variable sea ice landscape that encompasses near-complete coverage in winter to near-complete absence in summer. We demarcated 2 bowhead whale seasons based on movement behaviour identified from inflection points of polynomial regression analysis of movement rate: winter (28 December to 15 March, $16.6 \pm 2.65 \text{ km d}^{-1}$) and summer (27 June to 27 December, $31.9 \pm 1.05 \text{ km d}^{-1}$). Resource selection functions were used to evaluate bowhead whale seasonal selection of sea ice landscape (coverage, thickness, and floe size). Movement and habitat use differed between Nunavut tagging sites likely as a consequence of sexual and reproductive segregation. Whales selected relatively low ice coverage, thin ice, and small floe areas in winter close to the maximum ice extent, presumably to reduce risk of ice entrapment while remaining within ice. In contrast, whales selected high ice coverage, thick ice, and large floe size areas in summer, presumably to reduce risk of killer whale predation while providing enriched feeding opportunities. Our results indicate that this large-bodied animal can moderate use of the large-scale fluctuations in seasonal sea ice typical of polar environments.

KEY WORDS: Arctic · Climate change · Conservation · Foraging behavior · Habitat selection · Ice entrapment · Killer whales · Predation · Summer · Winter

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INTRODUCTION

Large body size confers many selective advantages, particularly for high-latitude environments, including the ability to endure fasting through seasonal periods of food shortages, ameliorate seasonal changes to confer relative safety from environmental perturbations, negotiate large-scale migration, and segregate intra-specific habitat use (Peters 1986, Owen-Smith 1988, Calder 1994, Lovegrove 2006). Larger body size has the advantage of allowing individuals to carry proportionately larger fat reserves, which is an adaptation to extremes in seasonality (e.g. fasting endurance; Lindstedt & Boyce 1985, Millar & Hickling 1990). Large body size is also associated with greater range that provides the flexibility to seasonally adjust habitat se-

lection and minimize environmental variation (Southwood 1977, Ferguson et al. 1999).

All 3 species of cetaceans that are year-round residents of the Arctic, beluga *Delphinapterus leucas*, narwhal *Monodon monoceros*, and bowhead *Balaena mysticetus*, are seasonal migrants that give birth and nurse their young during the spring, follow the receding ice into the high Arctic during summer, and migrate to the marginal ice during maximum ice extent in winter (see Laidre et al. 2008 and references therein). Although analysis of ice selection has provided an understanding of sea ice use (Laidre & Heide-Jørgensen 2005, Loseto et al. 2006, Moore & Laidre 2006), no quantitative analysis of ice habitat selection via disproportional use and/or availability has ever been conducted to test the general premise of seasonal selection.

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The bowhead whale is the only baleen whale endemic to the Arctic. They are characterized by the thickest blubber layer of any mammal (up to 50 cm), an advantage for the seasonal cycle of feeding and fasting characteristic of high-latitude life (Dyke et al. 1996). Large body size provides a selective advantage in seasonally ice-covered waters by minimizing the risk of ice entrapment, since bowheads can reportedly break ice 30 to 60 cm thick (Marquette 1986, Montague 1993, Würsig & Clark 1993). Large size and the associated scale of movements provide bowhead whales with exceptional movement abilities (Heide-Jørgensen et al. 2003a, 2006), a necessity in following the large-scale shifts in seasonal ice cover.

Prior to commercial whaling, bowhead whales had a circumpolar distribution and 5 stocks were thought to be geographically distinct (Burns et al. 1993). Since their evolutionary origin during the Pliocene, bowhead whale distribution ranged across the marine high latitudes, waxing and waning with glaciations (McLeod et al. 1993, Dyke et al. 1996). Bowhead whales of the Eastern Canada-West Greenland (EC-WG) population are assumed to spend the winter in Hudson Strait, northern Hudson Bay, or along the pack-ice edge extending to coastal West Greenland (Fig. 1) (Reeves & Heide-Jørgensen 1996, Koski et al. 2007). In spring, bowhead whales move from their winter range to the west coast

of Greenland, Foxe Basin, Cumberland Sound, and the entrance to Lancaster Sound. During the summer, bowhead whales are known to be widely distributed in the fjords and bays of the Canadian High Arctic, in Hudson Bay, Foxe Basin (Cosens et al. 1997, Cosens & Innes 2000, Higdon & Ferguson 2010), the Gulf of Boothia and Prince Regent Inlet (L. Dueck et al. unpubl. data). Bowhead whales feed primarily in late summer–fall on pelagic and epibenthic zooplankton (e.g. Finley 2001, Lowry et al. 2004) in areas that may be critical to their annual cycle of fat deposition and catabolism; however, reports of intensive feeding during late winter–early spring have been reported (Lee et al. 2005, Laidre et al. 2007). In fall, whales move south along the east coast of Baffin Island or cross over to the West Greenland coast (Reeves et al. 1983), whereas whales in Foxe Basin are thought to move south to east and winter in Hudson Strait (Reeves & Mitchell 1990).

Bowhead whale habitat use has typically been described in relation to sea ice. Bowhead whales can navigate through extensive areas of nearly solid sea ice cover (Ellison et al. 1987, George et al. 1989, Mate et al. 2000, Heide-Jørgensen et al. 2003a, 2006, Heide-Jørgensen & Laidre 2004). They use leads within sea ice, but prefer areas of loose ice (30 to 50% cover) and associated open water during summer (Reeves & Leatherwood 1985). Bowhead whales frequently spend

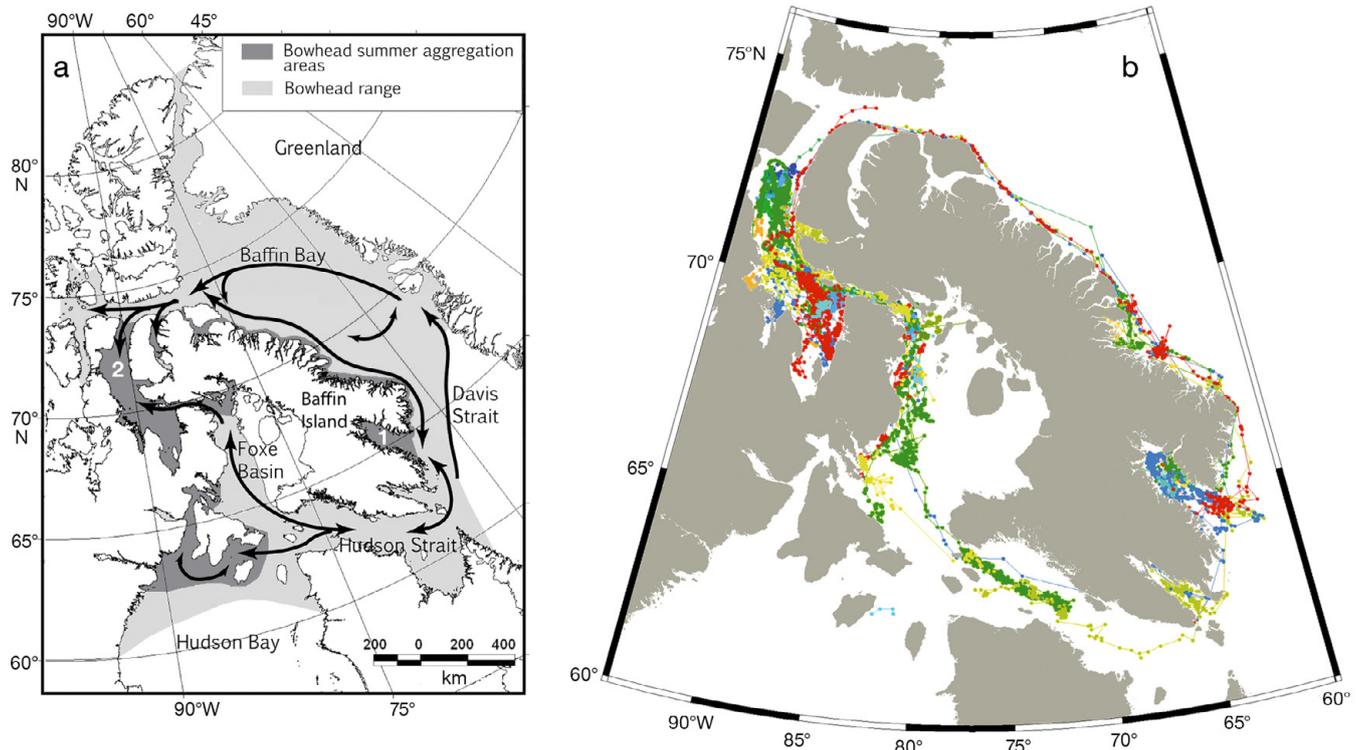


Fig. 1. Study area showing (a) general and (b) individual bowhead whale movements for the Eastern Canada-West Greenland population. In (a), 1 denotes Cumberland Sound and 2 Gulf of Boothia. In (b), colours represent individual whales ($n = 27$) estimated from satellite telemetry (only non-overlapping tracks visible)

time along the marginal ice zone in winter and early spring (Bogoslovskaya 2003), polynyas and the ice edge in late spring (Moore & Reeves 1993), and in summer and autumn select open water or light (40%) to moderate (70%) sea ice cover (Moore et al. 2000). They move southward with the advance of the seasonal pack ice in the late fall and move northward with annual ice retreat in the summer. As a result, annual migrations closely follow the oscillation of the floe edge.

Many authors have noted that each of the 3 ice-adapted Arctic whales (beluga, narwhal, and bowhead) extend their range into the high Arctic in summer following the retreat of sea ice and then during winter take refuge within 100s of kilometers of the margins of sea ice extent while avoiding the southern open-water regions (e.g. Mate et al. 2000, Moore et al. 2000, Heide-Jørgensen et al. 2003b, 2006, Laidre et al. 2004). Here we provide the first quantitative test of this seasonal sea ice selection for bowhead whales from the EC-WG population to address the question of whether bowhead whales select sea ice in summer during the ice retreat and reduced ice cover within the maximum sea ice extent in winter. First, we analyzed bowhead whale movement rates to determine the number and duration of behaviorally informed seasons that characterize their annual cycle. Second, we compared their seasonal use of sea ice habitat to test whether selection changes with the model derived movement seasons. Last, we considered how segregation of bowhead whales by sex and reproductive class may be associated with spatial and temporal variability of the Arctic sea ice environment. We discuss results in the context of major drivers (Power 1992) that include top-down forcing associated with predator avoidance, bottom-up forcing associated with foraging requirements, and avoiding risks of ice entrapment (Dueck & Ferguson 2009).

MATERIALS AND METHODS

Telemetry. Bowhead whales were tagged during the same period in July (5–18 July) in Foxe Basin in 2002 and 2003 and then in Cumberland Sound in 2004, 2005, and 2006 (Canadian Federal Government Animal Use Protocol: FWI-ACC-2004-012). Whales were approached by a small boat and instrumented with a satellite transmitter using an 8 m long fiberglass pole (Heide-Jørgensen et al. 2003a). Length was estimated by driving a boat (7.5 m) alongside the whale with people in the bow and stern, matching the tip of fluke with the stern and estimating total length relative to the bow. Age class and estimated length were strongly correlated ($r^2 = 0.890$; see Koski et al. 1993); therefore, we used length and did not include age categories

(results did not change qualitatively). Platform Transmitter Terminals were deployed (SPOT2 and SPOT3 transmitters, Wildlife Computers) with an expected longevity of 20 000 transmissions and were programmed to provide transmissions every day. Tags were programmed to transmit 4 times every day (6, 12, 18, and 24 h) and 3 to 23 transmissions were received each day (mean \pm SD = 9.27 ± 4.89). Locations were collected using the Argos System (see Harris et al. 1990), which provides location qualities with associated predicted accuracy. Location quality codes were B, A, 0, 1, 2, and 3 in order of increasing accuracy of position. The accuracy of location data from satellite tracking of pinnipeds was estimated (\pm SD) to be within 3.8 ± 2.6 km for class 0 positions, 18.8 ± 42.6 km for class A positions, and 22.8 ± 43.9 km for class B locations (Vincent et al. 2002), whereas the error of class 1, 2, and 3 quality codes is less than 1 km. Therefore, all class 0, 1, 2, and 3 location qualities were used to calculate an average daily position for each whale over the entire tracking period to minimize temporal autocorrelation (Oyer & Porter 2004) and to match the spatial resolution of our sea ice data. Distance and rate of travel for each whale were calculated using daily average positions as recommend by Tremblay et al. (2006).

Defining movement seasons. We defined seasons in order to assess sea ice selection by whales according to periods of similar movement behavior. First, we adjusted all distances according to the time between locations to remove the effect of a nonlinear relationship between time and distance (Ferguson & Elkie 2004). Specifically, the time–distance relationship was modeled using log-linear regression:

$$\ln(\text{distance} + 0.5) = m \times \ln(\text{time}) + \varepsilon \quad (1)$$

where ε is a random error and m is the regression coefficient (i.e. slope). The residuals of the log-linear regression (above) were used in a polynomial regression against day of the year (day), varying the number of coefficients from 1 to 12:

$$\text{residuals} = (\text{day})^1 + (\text{day})^2 + (\text{day})^3 + (\text{day})^4 + \dots + (\text{day})^{12} + \varepsilon \quad (2)$$

The residuals represent the distance traveled that cannot be explained by the log-linear relationship with $\ln(\text{time})$ elapsed and, therefore, we assume that the resulting discrepancy is due to a seasonal effect. We assessed the best fit model by adding successive coefficients to polynomial regressions and calculating Akaike's Information Criterion (AIC; Burnham & Anderson 1998). We calculated and compared corrected AIC (AIC_c) values for candidate models using SAS (SAS Institute 1998).

Movement seasons, defined as behaviorally informed, model-derived periods of time, were delineated by

the inflection point (i.e. second order derivative = 0) of the function defined by Eq. (2), which is indicative of a change in movement rate (km d^{-1}) from increasing to decreasing or vice versa, and thereby demarcated the beginning or end of movement seasons (Ferguson & Elkie 2004).

Sea ice selection. Habitat selection analysis requires standardized selection ratios of use and availability (Manly 1974). We used resource selection function models to assess selection of sea ice by bowhead whales (Boyce & McDonald 1999). Selection was defined as the use of a particular habitat type more often than expected relative to availability (Johnson 1980). Available habitat was determined by calculating the radius of a circle buffer equal to the 95th percentile distance traveled in one day for all individuals within a movement season (Rettie & Messier 2000). Based on the 95th percentile distance traveled, we created a circular buffer around each whale location with a radius of 96.3 km (median = 17.3, range 0.2 to 160.4 km) in summer and 56.7 km (median = 11.3, range 0.6 to 65.6 km) in winter. Habitat used was estimated according to the sea ice habitat type associated with the bowhead whale telemetry daily average location. Each whale location defined habitat used and was compared with the previous day's habitat location buffered by the distance we would reasonably (95th percentile) expect a whale to travel.

Canadian Ice Service (CIS) digital ice chart data over the eastern Canadian Arctic and Hudson Bay were used to determine bowhead whale use of ice types seasonally. CIS digital data are based on interpretation of RADARSAT-1, NOAA Advanced Very High Resolution Radiometer and Envisat Advanced Synthetic Aperture Radar, local observations, and aerial/marine surveys (Fequet 2002). The CIS data set provides a spatial resolution of approximately 1 km (Gagnon & Gough 2005) of sea ice stage of development information including classifications of sea ice concentration, thickness, and floe size, which comprised the focus of this analysis. Comparing telemetry location error (ca. 1 km) to median ice polygon size (8151 km^2) provided confidence in our habitat classification (White & Garrott 1990). CIS ice data were mapped out weekly except in the winter months (January to May) when they were mapped bi-weekly or monthly depending on requirements related to ship traffic safety. Whale location data was matched to the closest mid-point time for CIS ice maps.

CIS ice charts were imported into ArcGIS (version 8.3, Environmental Services Research Incorporated [ESRI]) as polygon shapefiles using polar stereographic projection. Telemetry locations were imported to create point files representing used habitat and buffers were created around locations representing available habitat. Ice characteristics for used and available habitats

were extracted using a polygon overlay method for further analyses. Available habitat within each circular buffer included all ice types as well as open water. Land area within availability buffers was subtracted from the total area of available habitat before creating the sea ice habitat categories and allowed for statistical independence of habitat categories (i.e. percentages do not add to 100, Fortin et al. 2005).

Four to 5 habitat categories were created for the 3 sea ice characteristics to provide a reasonable number of categories for statistical analyses. Sea ice concentrations were grouped into 4 categories as follows: open water (0–35% cover), mixed ice (35–65% ice cover), closing ice (65–95%), and closed ice (95–100%). Sea ice thickness included 5 categories: thin (0–30 cm), medium (30–70 cm), thick first year sea ice (70–120+ cm), old multiyear ice (>120 cm), and open water. For floe size, the 5 categories consisted of small floes (0–500 m), big floes (500–2000 m), very big floes (2–10+ km), landfast ice, and open water.

Utilization distribution. Kernel density estimators have been shown to be useful to quantify habitat use (Matthiopoulos 2003). We used density of location tracking data to identify areas of high use by bowhead whales. For locations less than 24 h apart, the path of the whale was interpolated at hourly intervals. If the interval between uplinks was more than 24 h, paths were not interpolated. Thus the interpolation method ensured that each trip was weighted by its duration in calculating density distributions. We did not use interpolations for uplinks greater than 24 h to minimize unrealistic linear interpolation through obstacles such as land and large uncertainty in the actual path of the whale given travel speeds of 20 to 50 km d^{-1} . We chose this approach since signal transmission likely varies with space and time. We used kernel density to identify core areas of utilization for conservation and therefore chose a coarse resolution of 0.5° for the density grid and a smoothing parameter of 15 km (Worton 1989, BirdLife International 2004), corresponding to the average error in Argos locations (Vincent et al. 2002). The 0.5° resolution is similar to that used in general circulation models adopted by the International Panel on Climate Change (IPCC 2007), and may thus be similar to that at which sea ice habitat selection occurs. A single density grid, representing the time spent (h) per unit area (km^2) by all whales combined at each cell of the grid was estimated from kernel analysis. A contour was defined across this grid to determine the areas where whales spent more than 95% of their time, which corresponds to the 95th quantile of the time spent per unit area (Pinaud & Weimerskirch 2007).

The density distributions are represented on maps as utilization distributions that were compared with typical sea ice conditions. Sea ice conditions were derived

from ice concentration maps of CIS normals (1970–2000, <http://ice-glaces.ec.gc.ca>). Considerable variation between years in the measured ice conditions is typical; however, we chose to compare whale utilization distributions and sea ice normals to provide general patterns of seasonal sea ice selection.

Population segregation based on movement rates and ice habitat selection. We tested whether bowhead whale movement rate differed with movement season, month, year, site of capture (Foxye Basin, Cumberland Sound), estimated length, sex (determined using genetic analysis of biopsy samples), and reproductive class (females with or without calves) using multivariate analysis of variance (MANOVA). We included individual whales as a random effect variable to control for individual variation and account for differences in sample sizes among tagged whales. All movement data were \log_{10} -transformed to normalize for parametric statistics. Only 1 d intervals were used to estimate movement rate (\log_{10} km d⁻¹) to avoid problems associated with a non-linear relationship between time and distance (Ferguson et al. 1998).

Statistical analysis. We used MANOVA to determine whether movement rate and habitat use were significantly different from random. For movement rates, we used MANOVA to test for differences relative to possi-

ble effects of tagging site, movement season, year, sex, length, and reproductive class of whales. Interaction terms were not considered due to data limitations. For habitat use, multiple dependent variables were beta values derived from the differences between the selection indices (b_i) for the habitat types, providing 4 to 5 resource selection values of sea ice characteristics (Arthur et al. 1996). The statistical procedure was analogous to a multivariate repeated-measures design and was applied separately to each sea ice metric examined: concentration, thickness, and floe size (Ferguson et al. 2000). MANOVA comparisons of resource selection functions compared site of tagging, sex, body length, and reproductive class (females with or without calves). Here we first stratified by movement season, then within season; each comparison was defined serially by site, sex, body length, and reproductive class. Data are presented as means \pm SE.

RESULTS

Twenty-seven bowhead whales from the EC-WG population were tagged with satellite transmitters from 2002 to 2006 (Table 1). A total of 5 females with calves were tagged and all were located in Foxye Basin

Table 1. *Balaena mysticetus*. Summary information of bowhead whales tagged in Foxye Basin (FB) and Cumberland Sound (CS). IM: immature male; IF: immature female; YM: young adult male; YF: young adult female; YC: young female with calf; LC: large female with calf; LM: large male; I: immature; Y: young; UK: unknown

| Year | Deployment location | Tag | Total locations | Last transmission date (dd/mm/yy) | Length (m) | Sex | Reproductive status |
|------|---------------------|--------|-----------------|-----------------------------------|------------|--------|---------------------|
| 2002 | FB | 13280 | 29 | 17/07/02 | 13 | Male | YM |
| | FB | 20685 | 111 | 27/09/02 | 12 | Male | YM |
| | FB | 37227 | 168 | 20/08/02 | 15 | Female | LC |
| | FB | 37228 | 244 | 10/09/02 | 14 | Female | YC |
| | FB | 246411 | 79 | 22/08/02 | 14 | Female | YF |
| 2003 | FB | 20160 | 71 | 25/07/03 | 15 | Female | LC |
| | FB | 21802 | 673 | 07/08/03 | 13 | Female | YC |
| | FB | 26712 | 140 | 08/08/03 | 12 | Female | IF |
| | FB | 37229 | 619 | 02/09/03 | 10 | Female | IF |
| | FB | 37230 | 396 | 18/09/03 | 11 | Female | IF |
| | FB | 37280 | 1919 | 27/11/03 | 17 | Female | LC |
| | FB | 201671 | 602 | 12/08/03 | 13 | Male | YM |
| | FB | 246412 | 38 | 20/09/03 | 11 | Female | IF |
| | CS | 20157 | 34 | 01/08/04 | 14 | Male | LM |
| 2004 | CS | 3965 | 21 | 13/08/05 | 11 | Male | IM |
| | CS | 20168 | 8 | 24/08/05 | 13 | Female | YF |
| 2005 | CS | 20687 | 327 | 03/09/05 | 9 | Male | IM |
| | CS | 201672 | 1148 | 06/02/06 | 11 | UK | UK (I) |
| 2006 | CS | 66351 | 151 | 17/09/06 | 10 | Female | IF |
| | CS | 66352 | 716 | 24/04/07 | 11 | Female | IF |
| | CS | 66353 | 1208 | 01/05/07 | 12 | Male | YM |
| | CS | 66354 | 91 | 06/08/06 | 13 | Male | YM |
| | CS | 66355 | 173 | 25/01/07 | 13.5 | UK | UK (Y) |
| | CS | 66356 | 568 | 28/11/06 | 12 | Male | YM |
| | CS | 66357 | 55 | 25/01/07 | UK | UK | UK |
| | CS | 66358 | 1246 | 24/11/06 | 9 | Male | IM |
| | CS | 66359 | 166 | 03/05/07 | 13 | Female | YF |

(Table 1). While whales moved throughout the study area, 2 circumnavigated Baffin Island and 6 overwintered in Hudson Strait, Cumberland Sound, and Davis Strait (Fig. 1).

Defining movement seasons

Distance moved was not linearly related to $\ln(\text{time})$ between telemetry locations ($\ln[\text{distance}] = 0.692[\ln(\text{days})] + 2.868$) with a slope (fractal dimension) of <1 ($F_{1,1369} = 79.1$, $p = 0.0001$). Thus, the logarithm of distance moved decreased non-linearly with increasing $\ln(\text{time})$ between locations. To control for this effect, we used residuals from the log-linear regression in the following analysis designed to objectively determine movement seasons. Residuals of distance moved against days of the year were best fitted to a 4th order polynomial ($r^2 = 0.218$) as determined by AIC_c , and inflection points demarcated 2 movement seasons (Fig. 2). Of the 365 d available in a year, we had telemetry locations for 308, thereby limiting our analyses to less than a full year. Also, temporal variation in number of locations resulted from loss of transmission over time. As a result, we interpret the finding of only 2 seasons as preliminary and more seasons may result from greater coverage.

Summer was characterized by high rates of movement ($31.9 \pm 1.05 \text{ km d}^{-1}$, $n = 970$) and lasted from 27 June to 27 December (184 d). In contrast, winter (78 d) occurred from 28 December to 15 March and was characterized by low movement rates ($16.6 \pm 2.65 \text{ km d}^{-1}$,

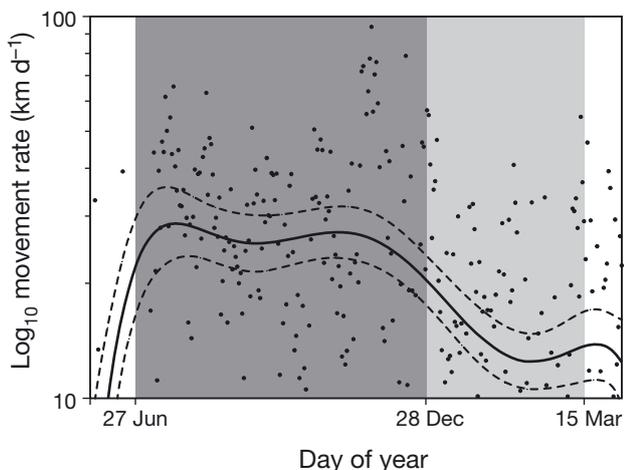


Fig. 2. *Balaena mysticetus*. Movement seasons of bowhead whales delineated using a log-linear polynomial regression model fitted to rate of movement ($\log_{10} \text{ km d}^{-1} \pm 95\%$ confidence interval) versus date. The corrected Akaike's Information Criterion selected a 4th order polynomial as best fitting the data, indicating 2 movement seasons demarcated by inflection points: summer, 27 June to 27 December (184 d), and winter, 28 December to 15 March (78 d)

$n = 153$). Differences in movement rates between the 2 movement seasons were significant ($F_{1,1121} = 29.0$, $p = 0.0001$). The remaining spring period (16 March to 26 June) was not sufficiently covered by the available data (3 whales and 219 locations) and was not used in subsequent analyses. There was some indication of 2 migratory bouts during the summer–autumn period indicated by peaks in movement rate that occurred around 22 July when whales moved from the spring to summer range and around 29 October when whales were returning from the summer to winter range. Also, a peak of movement occurred around 3 April that may reflect travel from the winter to spring range. Monthly differences in movement rates supported these seasonal distinctions with significantly higher movement rates in July ($37.6 \pm 2.24 \text{ km d}^{-1}$) and November ($44.2 \pm 2.68 \text{ km d}^{-1}$), whereas the lowest monthly rate was in February ($16.5 \pm 4.29 \text{ km d}^{-1}$; Fig. 3).

Whales tagged in Foxe Basin moved at the greatest rate during July ($36.2 \pm 2.56 \text{ km d}^{-1}$, $n = 137$) and the slowest during November ($13.3 \pm 8.65 \text{ km d}^{-1}$, $n = 12$; Fig. 3). In contrast, whales tagged in Cumberland Sound moved faster during November ($47.1 \pm 2.80 \text{ km d}^{-1}$, $n = 126$) and slowest during February ($16.5 \pm 4.28 \text{ km d}^{-1}$, $n = 54$) and April ($16.6 \pm 4.49 \text{ km d}^{-1}$, $n = 49$).

Sea ice selection

Overall, bowhead whales were less selective of ice concentration, thickness, and floe in summer compared to winter (Fig. 4). Bowhead whales selected high ice concentration ($>65\%$) in summer and, in contrast,

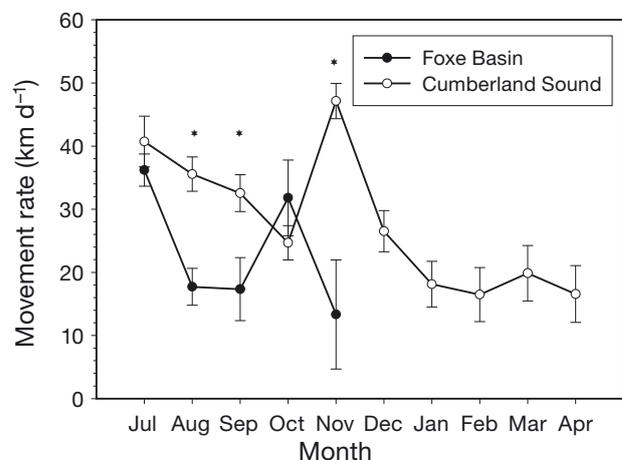


Fig. 3. *Balaena mysticetus*. Comparison of movement rates by month of bowhead whales tagged in Cumberland Sound and Foxe Basin (mean \pm SE). *Significance of the multiple range test. For Foxe Basin, July (highest) and November (lowest) are significantly different, while for Cumberland Sound, November (highest) and February (lowest) are significantly different

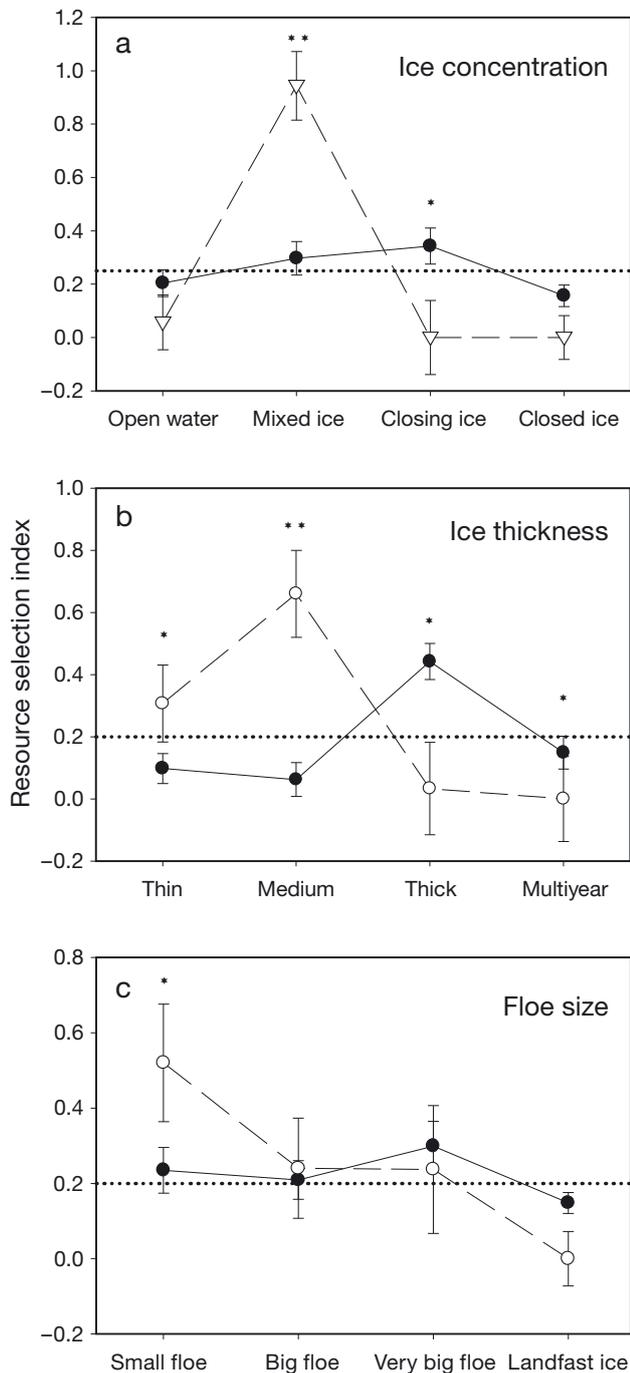


Fig. 4. Winter (dashed line) and summer (solid line) selection of ice types by bowhead whales based on resource selection function analysis. *Significance of the multiple range test. Values above the dotted horizontal line indicate preference and values below indicate avoidance. (a) Concentration of sea ice, where open water indicates relative selection of 0–35% ice coverage, mixed ice 35–65%, closing ice 65–95%, and closed ice 95–100%. (b) Thickness of sea ice, where thin is 0–30 cm, medium is 30–70 cm, thick is 70–120+ cm, and old multiyear ice is >120 cm. (c) Floe size, where small floes are 0–500 m, big floes are 500–2000 m, very big floes are 2–10 km, and landfast ice is sea ice solidly attached to the coast

selected 35–65% ice concentration in winter, while avoiding areas with >65% ice concentration. Similarly, in summer, bowhead whales selected thick first year ice (70–120+ cm) and open water, whereas in winter they selected thin and medium first year ice (0–70 cm) while avoiding open water, multiyear ice, and ice greater than 70 cm thick. For floe size, bowhead whales in winter selected small floe size (2–500 m) areas compared to summer use (Table 2). During both summer and winter movement seasons, whales avoided areas of large ice floes >2 km.

Bowhead whale distribution during the summer period coincided with typical distribution of annual and multi-annual sea ice that remained within the Arctic Archipelago, particularly in the Gulf of Boothia region (Fig. 5). During winter, bowhead whale distribution coincided with pockets of low sea ice concentration (35–65%) within 300 km of the maximum winter sea ice extent (Fig. 5b).

Segregation

Movement season, month, tagging site, length, and reproductive class differed in movement rate, whereas year and sex did not (Table 3). Whales tagged in Cumberland Sound traveled faster ($30.0 \pm 1.82 \text{ km d}^{-1}$) than whales tagged in Foxe Basin ($26.6 \pm 1.08 \text{ km d}^{-1}$). Longer whales (14–17 m) moved slower ($21.8 \pm 2.38 \text{ km d}^{-1}$, $n = 7$) compared to small (9–11 m, $30.6 \pm 1.32 \text{ km d}^{-1}$, $n = 9$) and medium sized whales (12–13 m, $30.1 \pm 1.55 \text{ km d}^{-1}$, $n = 10$). And females with calves

Table 2. Multivariate ANOVA tests for each of 3 ice indices (concentration, thickness, and floe size) with whales ($df = 24$) as dependent variables and b_i values (resource selection function) as random variables

| Ice index | <i>F</i> | <i>p</i> |
|-------------------------------|----------|----------|
| Sea ice concentration | | |
| Open (0–35%) | 1.66 | 0.21 |
| Mixed (35–65%) | 20.33 | 0.0001 |
| Closing (65–95%) | 4.94 | 0.036 |
| Closed (95–100%) | 2.90 | 0.10 |
| Sea ice thickness | | |
| Thin (0–30 cm) | 3.72 | 0.066 |
| Medium (30–70 cm) | 17.76 | 0.003 |
| Thick first-year (70–120+ cm) | 5.82 | 0.024 |
| Old multiyear (>120 cm) | 1.36 | 0.26 |
| Open water | 3.02 | 0.096 |
| Sea ice floe size | | |
| Small floes (0–500 m) | 3.14 | 0.089 |
| Big floes (500–2000 m) | 0.14 | 0.72 |
| Very big floes (2–10+ km) | 0.10 | 0.76 |
| Landfast ice | 2.38 | 0.14 |
| Open water | 1.89 | 0.18 |

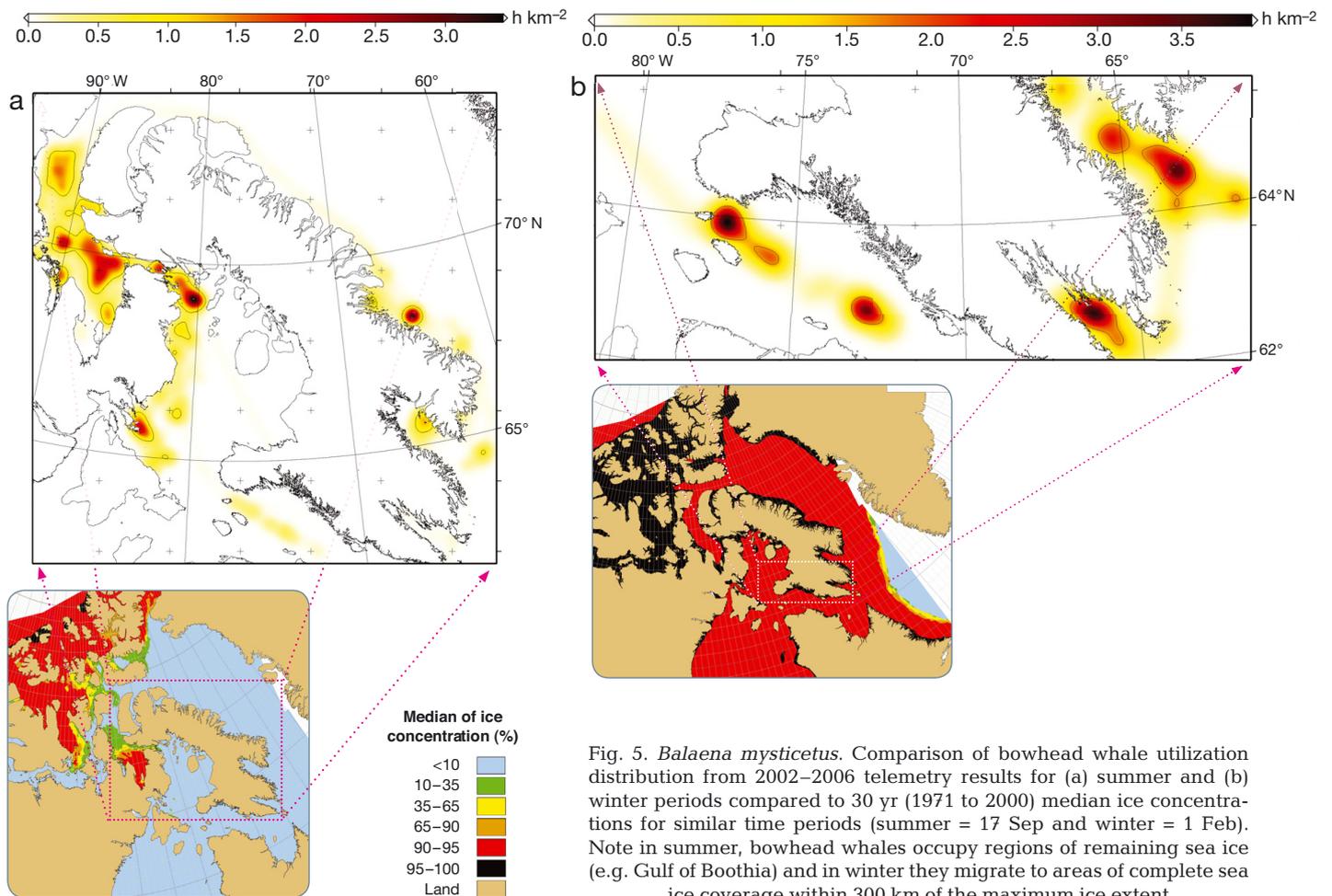


Fig. 5. *Balaena mysticetus*. Comparison of bowhead whale utilization distribution from 2002–2006 telemetry results for (a) summer and (b) winter periods compared to 30 yr (1971 to 2000) median ice concentrations for similar time periods (summer = 17 Sep and winter = 1 Feb). Note in summer, bowhead whales occupy regions of remaining sea ice (e.g. Gulf of Boothia) and in winter they migrate to areas of complete sea ice coverage within 300 km of the maximum ice extent

Table 3. Multivariate ANOVA (Model $F_{14,427} = 3.90$, $p = 0.0001$) of movement rate ($\log_{10} \text{ km d}^{-1}$) of bowhead whales in the eastern Canadian Arctic, 2002–2006, according to differences due to whale, movement season, year, month, tagging site, whale length, sex, and reproductive class (female with calf or female without)

| Comparison | df | F | p |
|--------------------|----|-------|--------|
| Whale | 13 | 3.38 | 0.0001 |
| Season | 1 | 10.71 | 0.0012 |
| Year | 3 | 0.93 | 0.395 |
| Month | 9 | 11.03 | 0.0001 |
| Site | 1 | 3.16 | 0.0001 |
| Length (m) | 2 | 2.70 | 0.0001 |
| Sex | 1 | 0.77 | 0.463 |
| Reproductive class | 1 | 3.39 | 0.0001 |

moved slower ($25.2 \pm 2.41 \text{ km d}^{-1}$, $n = 5$) than females without calves ($29.1 \pm 1.76 \text{ km d}^{-1}$, $n = 9$).

For sea ice selection during the summer movement season, few differences were observed among the 27 whales relative to tagging location and whale length, sex, and reproductive class (Table 4). No differences

between tagging sites were observed for ice concentration, but for ice thickness, whales tagged in Foxe Basin compared to Cumberland Sound selected thick (70–120+ cm) first year ice (resource selection function for Foxe Basin 0.63 ± 0.081 versus 0.31 ± 0.081 for Cumberland Sound) and avoided old (>120 cm) multi-year ice (0.063 ± 0.066 versus 0.26 ± 0.066 , respectively). For floe size, whales tagged in Foxe Basin compared to Cumberland Sound selected big floes (0.43 ± 0.073 versus 0.15 ± 0.073), whereas the opposite pattern was evident for small floes (Cumberland Sound, 0.081 ± 0.064 versus Foxe Basin, 0.37 ± 0.064). Last, females with calves were more commonly in landfast ice (0.20 ± 0.091) than were females without calves (0.05 ± 0.053).

For the winter movement season, only 6 whales were available for comparisons and only length and sex could be compared with no significant differences recorded. Despite the sample size limitations, these results were in accord with predictions that bowhead whales of all size and sex classes select similar sea ice habitat during winter.

Table 4. Multivariate ANOVA tests for each of 3 ice indices (concentration, thickness, floe size) with whales ($n = 27$) as dependent variables and b_i values (resource selection function) as random variables according to location (Foxe Basin and Cumberland Sound), length (3–15 m), sex (male or female), and reproductive class (females with or without calves). Significant differences indicated in **bold**

| Comparison | Model | | Location | | Length | | Sex | | Reproduction | |
|-------------------------------|----------|----------|-------------|--------------|----------|----------|----------|----------|--------------|-------------|
| | <i>F</i> | <i>p</i> | <i>F</i> | <i>p</i> | <i>F</i> | <i>p</i> | <i>F</i> | <i>p</i> | <i>F</i> | <i>p</i> |
| Sea ice concentration | | | | | | | | | | |
| Open (0–5%) | 0.73 | 0.68 | 0.92 | 0.36 | 1.04 | 0.46 | 0.04 | 0.83 | 0.07 | 0.79 |
| Mixed (35–65%) | 0.77 | 0.65 | 2.06 | 0.18 | 0.74 | 0.63 | 1.18 | 0.30 | 0.01 | 0.90 |
| Closing (65–95%) | 1.02 | 0.49 | 1.65 | 0.23 | 0.88 | 0.55 | 2.13 | 0.18 | 0.03 | 0.85 |
| Closed (95–100%) | 1.21 | 0.40 | 3.14 | 0.11 | 0.73 | 0.64 | 0.23 | 0.64 | 0.09 | 0.77 |
| Sea ice thickness | | | | | | | | | | |
| Thin (0–30 cm) | 0.62 | 0.76 | 2.14 | 0.18 | 0.57 | 0.74 | 0.11 | 0.75 | 0.04 | 0.85 |
| Medium (30–70 cm) | 0.76 | 0.66 | 1.85 | 0.21 | 0.89 | 0.54 | 0.03 | 0.86 | 0.27 | 0.62 |
| Thick first-year (70–120+ cm) | 1.19 | 0.41 | 6.27 | 0.036 | 0.83 | 0.57 | 0.01 | 0.91 | 0.03 | 0.86 |
| Old multiyear (>120 cm) | 0.57 | 0.80 | 7.48 | 0.015 | 0.43 | 0.84 | 0.00 | 0.94 | 0.63 | 0.45 |
| Open water | 0.90 | 0.57 | 1.37 | 0.27 | 1.08 | 0.44 | 0.25 | 0.63 | 0.60 | 0.46 |
| Sea ice floe size | | | | | | | | | | |
| Small (0–500 m) | 1.56 | 0.26 | 9.15 | 0.016 | 0.52 | 0.78 | 3.35 | 0.10 | 0.00 | 0.95 |
| Big (500–2000 m) | 1.12 | 0.44 | 0.10 | 0.75 | 1.01 | 0.48 | 1.74 | 0.22 | 0.17 | 0.69 |
| Very big (2–10+ km) | 2.13 | 0.14 | 10.78 | 0.011 | 1.63 | 0.25 | 0.30 | 0.60 | 0.13 | 0.72 |
| Landfast ice | 1.86 | 0.19 | 1.05 | 0.33 | 1.18 | 0.40 | 0.00 | 0.97 | 7.36 | 0.02 |
| Open water | 0.53 | 0.82 | 0.28 | 0.60 | 0.45 | 0.82 | 0.85 | 0.38 | 1.35 | 0.27 |

DISCUSSION

Bowhead whales of the EC-WG population seasonally move north and west into the Canadian Arctic Archipelago following the receding sea ice during the summer open-water season and then south and east into regions close to the southern margins of sea ice extent in winter (Fig. 5). Our results are the first to show that bowhead whales select more ice in summer and less ice in winter while remaining within the seasonal ice margin. Seasonal migration patterns were highlighted by relatively faster movements in July and October to reach distant areas between seasonal home ranges. Variation in movements ranged from 17 km d⁻¹ in winter to 47 km d⁻¹ during peak months. We consider how the seasonal sea ice habitat selection relates to requirements for food resources or avoiding predation.

With the onset of winter and sea ice growth, bowhead whales moved south to areas located within the sea ice extent but characterized by less ice concentration, thinner ice, and smaller floes, which are features of the sea ice that would minimize ice entrapment. Risk of ice entrapment plays a significant role in the evolution of bowhead whale migratory traditions and may partially explain their choice of winter range (George et al. 1989, Laidre & Heide-Jørgensen 2005). Wintering areas occur in Hudson Strait and the pack ice of Davis Strait for the EC-WG population (Reeves et al. 1983, Turl 1987, Dueck et al. 2006, Koski et al. 2007). Winter habitat use results characterized bowhead whales as selecting medium ice cover (35–65%), first-year ice (30–70 cm), and small ice floes (0–500 m) that may pro-

vide protection from predators generally by being located within the ice but far from the winter ice extent. Although adults are capable of avoiding ice entrapment (George et al. 1994), calves are born in late winter–early spring and these ice conditions likely minimize ice entrapment by newborn calves (Schell & Saupe 1993). In support of this conclusion, median sea ice in June, indicating areas of first ice break-up, coincided with bowhead whale winter distribution. With continued warming and reduction of sea ice extent, traditional bowhead whale winter areas may not have the requisite sea ice conditions. Therefore, if whales continue to use these areas in winter, they may be exposed to predation and competition from open-water adapted marine mammals (Dueck & Ferguson 2009).

Risk of killer whale *Orcinus orca* predation during different seasons and for different regions likely contributes to bowhead whale seasonal habitat selection (George et al. 1994, Corkeron & Connor 1999). For example, risk of killer whale encounters may explain why bowhead whales choose winter habitat within the sea ice rather than in open water located within 100s of kilometers of their winter range. Killer whales in the Arctic tend to avoid extensive sea ice possibly due to the damage ice could cause to their large dorsal fin and due to risk of ice entrapment. Killer whales annually visit some of the same regions of the Canadian Arctic that are used by bowhead whales during the open-water season, and there are several historical and recent reports of predation on bowhead whales in these areas (Reeves & Mitchell 1988). More recently, associated with decreasing sea ice in choke points

such as Hudson Strait (Higdon & Ferguson 2009), killer whale sightings have increased within the range of bowhead whales. Inuit Traditional Knowledge studies indicate increased killer whale attacks on bowhead whales in the Foxe Basin region where many juveniles and nursing females occur in spring (Ferguson et al. 2010). Bowhead whales are adapted to use a hide and, if caught, a fight strategy against killer whale attacks (Ford & Reeves 2008). Thus bowhead whales likely select specific sea ice habitat that provides safe cover to both avoid killer whales and, if detected, assist in fighting back.

Bowhead whales have sizeable energetic needs in support of their large body mass and therefore collocate with abundant food resources located at high densities during specific periods of the year. Thus, bowhead whales may select sea ice areas for foraging opportunities (Finley 2001). Between the open water and permanent ice cover, the marginal ice zone is the most productive area in the Arctic Ocean (Gosselin et al. 1997). These productive sites attract a large grazing zooplankton biomass (Sakshaug 1997), among which are the lipid-rich copepods and euphausiids (Percy & Fife 1980, Falk-Petersen et al. 1998) that are preyed on by bowhead whales (Marquette 1986, Lowry 1993). Bowhead whales have been observed feeding at the sea surface, within the water column, and benthically (Rogachev et al. 2008). Prey density is unlikely the key feature controlling migration patterns since bowhead whales abandon highly productive areas in the Bering Sea and West Greenland during the peak spring plankton bloom to move into less productive Beaufort Sea and Arctic Archipelago, respectively (Lowry 1993, Laidre et al. 2007). Other factors besides food and predator avoidance that may explain bowhead whale movement patterns include a behavioural preference for ice-edge habitat and the avoidance of competition for food from other baleen whales. In addition, EC-WG bowhead whales are currently harvested as part of subsistence hunts in both Canada and Greenland.

During the spring, adult bowhead whales appear in Disko Bay, where intensive feeding occurs for several weeks before moving across to the southern extent of the North Water (Heide-Jørgensen et al. 2006). Larger whales may forgo ice cover in favour of areas that concentrate zooplankton at depth. Such feeding behaviour is well documented at Isabella Bay, eastern Baffin Island, where adolescent and adult bowhead whales aggregate in autumn to feed on concentrations of copepods in deepwater troughs (Finley 2001). Although the east Baffin Bay segment of the EC-WG population may not be represented by this analysis, the Cumberland Sound segment of the population that was tagged in west Baffin Bay displayed movement behaviour that could be attributable to whales that

generally use Baffin Bay, both east and west, during late spring and summer. The Cumberland Sound tagged whales showed similar use of sea ice as Foxe Basin whales.

We discerned difference in movement rate and ice habitat selection between whales tagged in Cumberland Sound and Foxe Basin. The Foxe Basin nursery area (Cosens & Blouw 2003) is characterized by shallow waters and spring ice cover, providing safe and relatively calm waters with predictable oceanographic processes suitable for nursing, in contrast to other segments of the population that tend to occupy coastal areas around Baffin Bay during spring (Finley 2001). As sea ice melts, whales are likely exposed to increased vulnerability to predation as killer whales enter the area (Dueck & Ferguson 2009). Bowhead whales pass through Fury and Hecla into the extensive ice cover in Prince Regent Inlet and the Gulf of Boothia regions. In the Gulf of Boothia, sea ice persists during most summers, providing nursery habitat throughout the summer and fall period (Fig. 5). Thus for bowhead whales, the presence of suitable ice cover provides exclusion of killer whales and protection from predation of young while overwintering, calving and calf rearing, and foraging. Exclusion of killer whales by ice also provides opportunity for prolonged and undisturbed social encounters such as mating (Finley 2001). We did not discern differences in sea ice habitat selection due to sex and reproductive class (female with or without calf) between the 2 tagging sites.

The EC-WG bowhead whale population is highly segregated during much of the year. Northern Foxe Basin is considered to represent nursing habitat and, as a result, more females with calves and juveniles are present (Finley 2001). Specific habitat requirements differ between sex/age/reproductive classes, as suggested by population segregation (Cosens & Blouw 2003, Heide-Jørgensen et al. 2008). Bowhead whales are sexually dimorphic with females larger than males. Thus both sex- and age-related differences in habitat requirements are partly due to body size and include breath-holding capacity, which affects foraging strategy, vulnerability of smaller younger whales to killer whale predation, and ice entrapment due to size-related ability to break ice. Smaller bodied marine mammals, like seals, operate on an annual cycle of fat storage growth and reproduction (Boyd 2000). In contrast, larger-bodied whales operate on a 3 to 5 yr cycle of reproduction (Rugh et al. 1992, Oftedal 1997). This discrepancy requires research into body mass growth (fat deposition) and successful calf rearing to appropriately discriminate differences related to species body size.

Our results provide the first quantitative evidence of bowhead whale seasonal sea ice selection and raise important conservation questions on the future of bow-

head whales relative to global warming and loss of sea ice (Stroeve et al. 2008). Bowhead whales appear to be moderately sensitive to the anticipated climate-induced habitat alterations (Laidre et al. 2008) with the likelihood that they will show a seasonal mismatch between behavioural habitat use and recent changes in sea ice (Post et al. 2008). Climate change is likely to alter the quantity and quality of particular habitats and create contrary effects to eastern Arctic bowhead whale population viability. Assuming bowhead whales can track environmental change, continued loss of annual sea ice will result in an extension of bowhead whale habitat farther into the Archipelago, while contracting distances to suitable winter habitat, together offsetting overall changes in migration distances. In contrast, opportunities will increase for other competing whale species to extend their geographic range into areas currently used by bowhead whales, creating competition. Positive effects may include greater food availability as primary productivity increases with warmer temperatures (Grebmeier et al. 2006) and negative effects may include year-round risk of predation due to loss of sea ice as a predator refuge. The overall prediction is for the requisite Arctic sea ice habitat used by bowhead whales to eventually become limited as remaining sea ice diminishes towards the pole. The loose winter pack ice habitat of bowhead whales likely minimizes predation and ice entrapment while they await spring break-up and accessibility to feeding areas. With loss of sea ice, the spatial distribution of winter areas will change and how well bowhead whales can adapt their distribution accordingly remains unknown. Regions that currently support critical population processes, such as calving and over-winter survival, may not function as predator-relief habitat in the future with loss of sea ice.

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LITERATURE CITED

- Arthur SM, Manly BFJ, McDonald LL, Garner GW (1996) Assessing habitat selection when availability changes. *Ecology* 77:215–227
- BirdLife International (2004) Tracking ocean wanderers: the global distribution of albatrosses and petrels. Results from the Global Procellariiform Tracking Workshop, 1–5 Sep 2003, Gordon's Bay, South Africa. BirdLife International, Cambridge, available at www.birdlife.org/action/science/species/seabirds/tracking.html
- Bogoslovskaya L (2003) The bowhead whale off Chukotka: integration of scientific and traditional knowledge. In: McCartney AP (ed) Indigenous ways to the present: native whaling in the western Arctic. Studies in Whaling No. 6. Canadian Circumpolar Institute Press, Salt Lake City, UT, p 209–254
- Boyce MS, McDonald LL (1999) Relating populations to habitats using resource selection functions. *Trends Ecol Evol* 14:268–272
- Boyd IL (2000) State-dependent fertility in pinnipeds: contrasting capital and income breeders. *Funct Ecol* 14:623–630
- Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer, New York, NY
- Burns JJ, Montague JJ, Cowles CJ (eds) (1993) The bowhead whale. Spec Publ 2, The Society for Marine Mammalogy, Lawrence, KS
- Calder WA III (1984) Size, function, and life history. University of Chicago Press, Chicago, IL
- Corkeron PJ, Connor RC (1999) Why do baleen whales migrate? *Mar Mamm Sci* 15:1228–1245
- Cosens SE, Blouw A (2003) Size- and age-class segregation of bowhead whales summering in Northern Foxe Basin: a photogrammetric analysis. *Mar Mamm Sci* 19:284–296
- Cosens SE, Innes S (2000) Distribution and numbers of bowhead whales (*Balaena mysticetus*) in Northwestern Hudson Bay in August 1995. *Arctic* 53:36–41
- Cosens SE, Qamukaq T, Parker B, Dueck LP, Anadjuak B (1997) The distribution and numbers of bowhead whales, *Balaena mysticetus*, in northern Foxe Basin in 1994. *Can Field Nat* 111:381–388
- Dueck L, Ferguson SH (2009) Habitat use by bowhead whales (*Balaena mysticetus*) of the Eastern Canadian Arctic. Canadian Science Advisory Secretariat Research Document 2008/082, Fisheries and Oceans Canada, Winnipeg, Manitoba
- Dueck LP, Hiede-Jørgensen MP, Jensen MV, Postma LD (2006) Update on investigations of bowhead whale (*Balaena mysticetus*) movements in the eastern Arctic, 2003–2005, based on satellite-linked telemetry. Canadian Science Advisory Secretariat Research Document 2006/050, Fisheries and Oceans Canada, Winnipeg, Manitoba
- Dyke AS, Hooper J, Savelle JM (1996) A history of sea ice in the Canadian Arctic Archipelago based on postglacial remains of the bowhead whale (*Balaena mysticetus*). *Arctic* 49:235–255
- Ellison WT, Sonntag RM, Clark CW (1987) Potential use of surface reverberation by bowhead whales, *Balaena mysticetus*, in under-ice navigation: preliminary considerations. *Rep Int Whaling Comm* 37:309–312
- Falk-Petersen S, Sargent JR, Henderson J, Hegseth EN, Hop H, Okolodkov YB (1998) Lipids and fatty acids in the ice algae and phytoplankton from the Marginal Ice Zone in the Barents Sea. *Polar Biol* 20:41–47
- Fequet D (ed) (2002) MANICE: manual of standard procedures for observing and reporting ice conditions, 9th edn. Canadian Ice Service, Environment Canada, Ottawa
- Ferguson SH, Elkie PC (2004) Seasonal movement patterns of woodland caribou *Rangifer tarandus caribou*. *J Zool* 262: 125–134
- Ferguson SH, Rettie WJ, Messier F (1998) Fractal measures of female caribou movements. *Rangifer* 10(Spec Issue): 139–147
- Ferguson SH, Taylor MK, Born EW, Rosing-Asvid A, Messier F (1999) Determinants of range size in polar bears (*Ursus maritimus*). *Ecol Lett* 2:311–318

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- Ferguson SH, Taylor MK, Messier F (2000) Influence of sea ice dynamics on habitat selection by polar bears. *Ecology* 81:761–772
- Ferguson SH, Higdon JW, Chmelnsky EG (2010) The rise of killer whales as a major Arctic predator. In: Ferguson SH, Loseto LL, Mallory ML (eds) *A little less Arctic: top predators in the world's largest northern inland sea*, Hudson Bay. Springer, New York, NY, p 117–136
- Finley KJ (2001) Natural history and conservation of the Greenland whale, or bowhead, in the Northwest Atlantic. *Arctic* 54:55–76
- Ford JKB, Reeves RR (2008) Fight or flight: antipredator strategies of baleen whales. *Mammal Rev* 38:50–86
- Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330
- Gagnon AS, Gough WA (2005) Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. *Arctic* 58:370–382
- George JC, Clark C, Carrol GM, Ellison WT (1989) Observations on the ice-breaking and ice navigation behavior of migrating bowhead whales (*Balaena mysticetus*) near Point Barrow, Alaska, spring 1985. *Arctic* 42:24–30
- George JC, Philo LM, Hazard K, Withrow D, Carroll GM, Suydam R (1994) Frequency of killer whale (*Orcinus orca*) attacks and ship collisions based on scarring on bowhead whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort Seas stock. *Arctic* 47:247–255
- Gosselin G, Levasseur M, Wheeler PA, Horner RA, Booth BC (1997) New measurements of phytoplankton and ice algal production in the Arctic Ocean. *Deep-Sea Res II* 44:1623–1644
- Grebmeier JM, Overland JE, Moore SE, Farley EV and others (2006) A major ecosystem shift in the Northern Bering Sea. *Science* 311:1461–1464
- Harris RB, Fancy SG, Douglas DC, Garner GW, Amstrup SC, McCabe TR, Pank LF (1990) Tracking wildlife by satellite: current systems and performance. *Fish Wildl Tech Rep* 30. US Department of the Interior, Fish and Wildlife Service, Washington, DC
- Heide-Jørgensen MP, Laidre KL (2004) Declining open water refugia for top predators in Baffin Bay and adjacent waters. *Ambio* 33:488–495
- Heide-Jørgensen MP, Laidre KL, Wiig Ø, Jensen MV and others (2003a) From Greenland to Canada in ten days: tracks of bowhead whales, *Balaena mysticetus*, across Baffin Bay. *Arctic* 56:21–30
- Heide-Jørgensen MP, Richard P, Dietz R, Laidre KL, Orr J, Schmidt HC (2003b) An estimate of the fraction of belugas (*Delphinapterus leucas*) in the Canadian high Arctic that winter in West Greenland. *Polar Biol* 26:318–326
- Heide-Jørgensen MP, Laidre KL, Jensen MV, Dueck L, Postma LD (2006) Dissolving stock discreteness with satellite tracking: bowhead whales in Baffin Bay. *Mar Mamm Sci* 22:34–45
- Heide-Jørgensen MP, Laidre KL, Wiig Ø, Bachmann L, Postma L, Dueck L (2008) Segregation of sexes and plasticity in site selection of bowhead whales. Paper SC/60/BRG19 presented to the International Whaling Commission Scientific Committee Meeting Santiago, Chile, June 2008. Available at www.iwcoffice.org
- Higdon JW, Ferguson SH (2009) Loss of Arctic sea ice causing punctuated change in sightings of killer whales (*Orcinus orca*) over the past century. *Ecol Appl* 19:1365–1375
- Higdon JW, Ferguson SH (2010) Past, present, and future for bowhead whales (*Balaena mysticetus*). In: Ferguson SH, Loseto LL, Mallory ML (eds) *A little less Arctic: top predators in the world's largest northern inland sea*, Hudson Bay. Springer, New York, NY, p 159–177
- IPCC (2007) *Climate change 2007: the physical science basis*. Solomon S, Qin D, Manning M, Marquis M, Averyt KB, Tignor M, Miller HL (eds) *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71
- Koski WR, Davis RA, Miller GW, Withrow DE (1993) Reproduction. In: Burns JJ, Montague JJ, Cowles CJ (eds) *The bowhead whale*. Special Publication No. 2, Society for Marine Mammalogy, Lawrence, KS, p 239–274
- Koski WR, Heide-Jørgensen MP, Laidre KL (2007) Winter abundance of bowhead whales, *Balaena mysticetus*, in the Hudson Strait, March 1981. *J Cetacean Res Manage* 8:139–144
- Laidre KL, Heide-Jørgensen MP (2005) Arctic sea ice trends and narwhal vulnerability. *Biol Conserv* 121:509–517
- Laidre KL, Heide-Jørgensen MP, Jørgensen OA, Treble MA (2004) Deep ocean predation by a high Arctic cetacean. *ICES J Mar Sci* 61:430–440
- Laidre KL, Heide-Jørgensen MP, Nielsen TG (2007) Role of the bowhead whale as a predator in West Greenland. *Mar Ecol Prog Ser* 346:285–297
- Laidre KL, Stirling I, Lowry LF, Wiig Ø, Heide-Jørgensen MP, Ferguson SH (2008) Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecol Appl* 18:S97–S125
- Lee SH, Schell DM, McDonald TL, Richardson WJ (2005) Regional and seasonal feeding by bowhead whales *Balaena mysticetus* as indicated by stable isotope ratios. *Mar Ecol Prog Ser* 285:271–287
- Lindstedt SL, Boyce MS (1985) Seasonality, fasting endurance, and body size in mammals. *Am Nat* 125:873–878
- Loseto L, Richard P, Orr J, Stern G, Ferguson SH (2006) Intrapopulation habitat selection by beluga whales in the eastern Beaufort Sea. *Can J Zool* 84:1743–1751
- Lovegrove BG (2006) The power of fitness in mammals: perceptions from the African slipstream. *Physiol Biochem Zool* 79:224–236
- Lowry LF (1993) Foods and feeding ecology. In: Burns JJ, Montague JJ, Cowles CJ (eds) *The bowhead whale*. Special Publication No. 2, Society for Marine Mammalogy, Lawrence, KS, p 201–238
- Lowry LF, Sheffield G, George JC (2004) Bowhead whale feeding in the Alaskan Beaufort Sea based on stomach contents analyses. *J Cetacean Res Manage* 6:215–223
- Manly BFJ (1974) A model for certain types of selection experiments. *Biometrics* 30:281–294
- Marquette WM (1986) Bowhead whale. In: Haley D (ed) *Marine mammals of the eastern North Pacific and Arctic Waters*, 2nd edn. Pacific Search Press, Seattle, WA, p 83–93
- Mate BR, Krutzikowsky GK, Winsor MH (2000) Satellite-monitored movements of radio-tagged bowhead whales in the Beaufort and Chukchi Seas during the late summer feeding season and fall migration. *Can J Zool* 78:1168–1181
- Matthiopoulos J (2003) Model-supervised kernel smoothing for the estimation of spatial usage. *Oikos* 102:367–377
- McLeod SA, Whitmore FC Jr, Barnes LG (1993) Evolutionary relationships and classification. In: Burns JJ, Montague JJ, Cowles CJ (eds) *The bowhead whale*. Special Publication

- No. 2, Society for Marine Mammalogy, Lawrence, KS, p 45–70
- Millar JS, Hickling GJ (1990) Fasting endurance and the evolution of mammalian body size. *Funct Ecol* 4:5–12
- Montague JJ (1993) Introduction. In: Burns JJ, Montague JJ, Cowles CJ (eds) *The bowhead whale*. Special Publication No. 2, Society for Marine Mammalogy, Lawrence, KS, p 1–21
- Moore SE, Laidre KL (2006) Trends in sea ice cover within habitats used by bowhead whales in the Western Arctic. *Ecol Appl* 16:932–944
- Moore SE, Reeves RR (1993) Distribution and movement. In: Burns JJ, Montague JJ, Cowles CJ (eds) *The bowhead whale*. Special Publication No. 2, Society for Marine Mammalogy, Lawrence, KS, p 313–386
- Moore SE, Demaster DP, Dayton PK (2000) Cetacean habitat selection in the Alaskan Arctic during summer and autumn. *Arctic* 53:432–447
- Oftedal OT (1997) Lactation in whales and dolphins: evidence of divergence between baleen- and toothed-species. *J Mammary Gland Biol Neoplasia* 2:205–230
- Owen-Smith RN (1988) Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge
- Oyer AM, Porter WF (2004) Localized management of white-tailed deer in the central Adirondack Mountains, New York. *J Wildl Manag* 68:257–265
- Percy JA, Fife FJ (1980) The proximate composition and caloric content of Arctic marine invertebrates from Fro-bisher Bay. *Can Data Rep Fish Aquat Sci* 214:1–35
- Peters RH (1986) Ecological implications of body size. Cambridge University Press, Cambridge
- Pinaud D, Weimerskirch H (2007) At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *J Anim Ecol* 76:9–19
- Post E, Pedersen C, Wilmers CC, Forchhammer MC (2008) Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. *Proc R Soc Lond B* 275:2005–2013
- Power ME (1992) Top-down and bottom-up forces in food webs: Do plants have primacy? *Ecology* 73:733–746
- Reeves RR, Heide-Jørgensen MP (1996) Recent status of bowhead whales, *Balaena mysticetus*, in the wintering grounds off West Greenland. *Polar Res* 15:115–125
- Reeves R, Leatherwood S (1985) Bowhead whale, *Balaena mysticetus* Linnaeus, 1758. In: Ridgway SH, Harrison RJ (eds) *Handbook of marine mammals: the sirenians and baleen whales*. Academic Press, London, p 305–344
- Reeves R, Mitchell E (1988) Distribution and seasonality of killer whales in the eastern Canadian Arctic. *Rit Fiskid* 11:136–160
- Reeves RR, Mitchell E (1990) Bowhead whales in Hudson Bay, Hudson Strait, and Foxe Basin: a review. *Can Field Nat* 117:25–43
- Reeves R, Mitchell E, Mansfield A, McLaughlin M (1983) Distribution and migration of the bowhead whale, *Balaena mysticetus*, in the Eastern North American Arctic. *Arctic* 36:5–64
- Rettie WJ, Messier F (2000) Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466–478
- Rogachev KA, Carmack EC, Foreman MGG (2008) Bowhead whales feed on plankton concentrated by estuarine and tidal currents in Academy Bay, Sea of Okhotsk. *Cont Shelf Res* 28:1811–1826
- Rugh DJ, Miller GW, Withrow DE, Koski WR (1992) Calving intervals of bowhead whales established through photographic identifications. *J Mammal* 73:487–490
- Sakshaug E (1997) Biomass and productivity distributions and their variability in the Barents Sea. *ICES J Mar Sci* 54:341–350
- SAS Institute (1998) Statistical analysis system, version 6.12. SAS Institute, Cary, NC
- Schell DM, Saupe SM (1993) Feeding and growth as indicated by stable isotopes. In: Burns JJ, Montague JJ, Cowles CJ (eds) *The bowhead whale*. Special Publication No. 2, Society for Marine Mammalogy, Lawrence, KS, p 491–509
- Southwood TRE (1977) Habitat, the templet for ecological strategies? *J Anim Ecol* 46:337–365
- Stroeve J, Serreze M, Drobot S, Gearheard S and others (2008) Arctic sea ice extent plummets in 2007. *EOS Trans Am Geophys Union* 89:13–14
- Tremblay Y, Shaffer SA, Fowler SL, Kuhn PE and others (2006) Interpolation of animal tracking data in a fluid environment. *J Exp Biol* 209:128–140
- Turl CW (1987) Winter sightings of marine mammals in Arctic pack ice. *Arctic* 40:219–220
- Vincent C, McConnell BJ, Ridoux V, Fedak MA (2002) Assessment of Argos location accuracy from satellite tags deployed on captive grey seals. *Mar Mamm Sci* 18:156–166
- White GC, Garrott RA (1990) Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168
- Würsig B, Clark C (1993) Behavior. In: Burns JJ, Montague JJ, Cowles CJ (eds) *The bowhead whale*. Special Publication No. 2, Society for Marine Mammalogy, Lawrence, KS, p 57–199

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