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Habitat Use by Bowhead Whales (*Balaena mysticetus*) of the Eastern Canadian Arctic

Utilisation de l'habitat par les baleines boréales (*Balaena mysticetus*) de l'est de l'Arctique canadien

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ABSTRACT

Bowhead whales (*Balaena mysticetus*) in the eastern Canadian Arctic were designated as Threatened by COSEWIC in May 2005. The primary reason for the historic collapse and Threatened designation of this population was an intensive commercial harvest which took place primarily during the 19th century. Here, we provide a review of relevant information available regarding bowhead habitat, by describing the features that characterize bowhead habitat, and evaluating to the extent possible, the quantity and quality of habitat used by bowheads, the biological functions served by different habitats, and existing or potential threats to habitat or access to habitat. Using habitat utilization distributions based on telemetry results for 2002-2006, we describe bowhead whale habitat use in the eastern Canadian Arctic relative to seasonal movements and possible functions of habitats selected. We discuss research necessary to provide the information on habitat relationships required to properly designate “critical” habitat for eastern Arctic bowhead whales.

RÉSUMÉ

Les baleines boréales (*Balaena mysticetus*) dans l'est de l'Arctique canadien ont été désignées comme étant menacées par le Comité sur la situation des espèces en péril au Canada (COSEPAC) en mai 2005. La principale raison de l'effondrement historique et de la désignation « menacée » de cette population consiste en une chasse commerciale intensive qui a eu lieu principalement au cours du 19e siècle. Nous offrons ici un examen de l’information pertinente disponible concernant l'habitat des baleines boréales, en décrivant les caractéristiques de l'habitat de la baleine boréale et en évaluant, dans la mesure du possible, la quantité et la qualité de l'habitat utilisé par les baleines boréales, les fonctions biologiques servies par différents habitats et les menaces actuelles ou éventuelles à l'habitat ou à l'accès à l'habitat. Au moyen des distributions d'utilisation de l'habitat fondées sur les résultats de la télémétrie de 2002 à 2006, nous décrivons l'utilisation de l'habitat des baleines boréales dans l'est de l'Arctique canadien par rapport aux déplacements saisonniers et aux fonctions possibles des habitats sélectionnés. Nous discutons des recherches nécessaires pour fournir l'information sur les relations entre les habitats afin de désigner de façon appropriée l'habitat « essentiel » aux baleines boréales de l'est de l'Arctique.

INTRODUCTION

Bowhead whales are a species highly adapted to life in ice covered waters while making seasonal migrations to preferred habitat (Dyke *et al.* 1996, Moore 2000, Moore *et al.* 2000). The distribution and migrations of bowheads in the eastern Canadian Arctic (Fig. 1) are closely linked with the seasonal changes in sea ice (Eschricht and Reinhardt 1866, NWMB 2000, Reeves *et al.* 1983). From wintering areas in Hudson Strait and the pack ice of Davis Strait (Reeves *et al.* 1983, Turl 1987, Dueck *et al.* 2006, Koski *et al.* 2006), bowheads move north by several routes following the receding ice to spring and then summering areas along the west coast of Baffin Island and into the Arctic archipelago. In early spring, a segment of the bowhead population takes a route along the western coast of Greenland to Disko Bay, then across to the expanding southern margin of the North Water polynya (Eschricht and Reinhardt 1866, Heide-Jorgensen *et al.* 2003). Another route brings whales north along the east coast of Baffin Island and a third route used by another segment of the population moves west through Hudson Strait to polynyas in northwestern Hudson Bay and northern Foxe Basin (Reeves *et al.* 1983, Dueck *et al.* 2006). Spring movements provide two significant functions. First, by moving through ice of >90% cover (Fig. 2), bowheads may reduce the risk of encounters with killer whales (*Orcinus orca*). Second, the polynyas may provide abundant food during the early open-water season where the first bloom of productivity is initiated (Holst and Stirling 1999, Thomas 1999). As winter sea ice progressively diminishes, segments of the bowhead population in the regions of northern Foxe Basin and Lancaster Sound continue to move further into the archipelago (Dueck *et al.* 2006) while a third segment of the population moves along the coast of eastern Baffin Island (Finley et al. 1993, Heide-Jorgensen *et al.* 2003). Fall migrations southward occur (1) along the east Baffin Island coast and (2) through Fury and Hecla Strait and Foxe Basin, bringing whales once again to wintering areas in the vicinity of Hudson Strait.

Arctic species such as bowhead are well-adapted to the great variability characteristic of polar environments (Ferguson and Messier 1996). As a large, long-lived marine mammal (George et al. 1999), bowhead whales are capable of integrating environmental change over seasons and years and able to adapt behaviourly or physiologically. Large blubber resources built up over months and years may allow bowheads to survive extended periods of fasting (Lindstedt and Boyce 1985). This suggests that bowheads may be quite flexible and adaptable to changes in the temporal or spatial availability of suitable foraging habitat. The limits, physiological plasticity, and life-history consequences of this flexibility are critical to understanding habitat use but are largely unknown. Permanent or extended periods of loss of, or access to, important habitats over time could reduce the health or recovery rate of the population, through decreased energy uptake (loss of feeding habitat), or increased vulnerability to predation (loss of cover habitat). Reduced individual health through loss of energy may be observed as decreased population productivity (later age at maturation, longer interbirth interval, lower calf/juvenile survival); whereas predation effects are likely manifested as a change in age structure (loss of calves and juveniles). Quantification of these affects is necessary for evaluating habitat selection but will be challenging.

BACKGROUND

We describe current knowledge of seasonal bowhead movements while considering three key drivers: food availability, sea ice, and predation that vary according to strong seasonal fluctuations. We believe these three drivers provide a reasonably complete, while simplified, view of seasonal movements and habitat selection by bowheads and together explain critical processes required to manage bowhead habitat requirements. This view is based on basic ecological tenets that populations are commonly regulated both from above (top down predation) and below (bottom up food) (Sinclair 1989; Hunter and Price 1992) and involve both biotic and abiotic processes (Nicholson 1933). This overview provides a summary of eastern Arctic bowhead habitat use and possible habitat functions.

Biological features that characterize bowhead habitat use

We consider two key biological features that define the characteristics of bowhead whale habitat: (1) energy acquisition or feeding ecology related to reproduction and indirect survival and (2) direct mortality by selecting habitat that reduces risk of ice entrapment and predation by killer whales. With regard to general feeding ecology, bowhead whales are highly evolved filter feeders (McLeod *et al.* 1993), slow steady swimmers adapted for foraging on concentrated prey (Lowry 1993, Woodward *et al.* 2006). Bowheads alternate foraging behaviour between (1) obtaining a significant proportion of their annual energy requirements by feeding intensively in areas of concentrated prey during relatively brief but predictable seasonal periods, (2) foraging opportunistically during migration or other times for hours or several days, and (3) fasting for extended periods (Schell et al. 1989, Lowry 1993, Hobson and Schell 1998). Habitat features that provide seasonal concentrated sources of zooplankton (Finley *et al.* 1993, Lowry 1993) are thus most likely important features that define critical habitat for bowhead whales from spring to fall periods (Schell 2000).

Specific habitat requirements likely differ between sex/age/reproductive classes, as suggested by population segregation (Cosens and Blouw 2003, Heide-Jørgensen et al. 2008). Bowheads 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. For example, younger whales are limited to feeding at shallow depths due to limited breath-holding capacity. Although zooplankton is typically exploited by bowheads at relatively shallow depths by all age classes for parts of the year, seasonal concentrations of zooplankton at greater depth may be available only to large whales (Laidre et al. 2007, Thomas 1999).

Newborn and young whales are particularly vulnerable to predation (NWMB 2000). Juveniles and females with young presumably use habitat that provides cover from killer whales thereby reducing the risk of predation. We consider that such areas would be characterized by either extensive ice cover or landscape. For the latter, complex coastal areas and waters that are less accessible due to narrow entrance passages may reduce the likelihood of encounters with, or detection by, killer whales. The “nursery” segment of the eastern Arctic bowhead population has been documented in northern Foxe Basin in spring (June – mid July) (Cosens *et al.* 1997, Cosens and Blouw 2003), a relatively shallow area of less than 100m depth, surrounded by heavy ice, with a current from Fury and Hecla Strait that presumably supplies nutrients for an enhanced spring plankton bloom (Fig. 2). Foxe Basin is connected to the Gulf of Boothia by Fury and Hecla Strait (ca. 160 km long, 16-24 km wide) which most probably is not negotiated by killer whales (Dyke et al. 1996). As ice break-up occurs, most of the “nursery” whales move through Fury and Hecla Strait to Prince Regent Inlet and Gulf of Boothia, an important summering area that provides consistent ice cover for the duration of the summer (Fig. 3). Killer whales have historically been present in Davis Strait and Baffin Bay and were often reported by whalers in the 1800s (Reeves and Mitchell 1988). However killer whales were not historically present in Hudson Bay and were not reported there until the mid-1900s (Degerbol and Freuchen 1935, Gonzales 2001, Higdon and Ferguson *In press*). Killer whales are now seen in Hudson Bay on a regular basis, as a response to declining ice conditions in Hudson Strait (Higdon and Ferguson *In press*). Reasonable conjectures as to why northern Foxe Basin and northwest Hudson Bay evolved as nursery areas (Cosens and Blouw 2003, Reeves and Cosens 2003) include the historical lack of killer whales as predators (Higdon 2007) and the presence of shallow water habitat that allows for effective foraging by depth-limited juveniles and females with young.

Adult bowheads appear during spring in Disko Bay, where feeding occurs intensively for several weeks before moving across to the southern extent of the North Water (Heide-Jørgensen et al. 2006). Disko Bay is one of the only areas in spring not completely surrounded by heavy ice in spring (Fig. 2), suggesting that large adults may risk encounters with killer whales to exploit resources in this area. Five species of baleen whales, including the bowhead whale, show *fight*-type reactions to killer whales (Ford and Reeves 2008). On the other hand, bowheads appear to move out of the Disko Bay area prior to peak zooplankton abundance (Heide-Jorgensen et al. 2007) suggesting that bowheads may vacate the area before the arrival of killer whales or alternatively to access more profitable distant feeding destinations. After moving over to the southern margin of the North Water, some of these whales continue to range along the eastern coast of Baffin Island during the summer, an area of variable ice cover and typically more open than the archipelago (Heide-Jørgensen et al. 2006).

Vertical migration of copepods results in larger-sized individuals with higher energy content accumulating in deeper waters (Longhurst *et al.* 1984, Heide-Jorgensen et al. 2006, Michaud and Taggart 2007). 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. Here, large adolescent and adult bowhead whales aggregate in autumn to exploit concentrations of copepods in deepwater troughs (Finley et al. 1993). The extent of this behaviour in other areas along eastern Baffin Island or elsewhere is unknown. Isabella Bay is situated at the south end of the longest expanse of shallow waters on the east coast of Baffin Island (Finley *et al.* 1993), and as such, this specific site may provide habitat that is seasonally important. Another potential area of similar oceanographic processes occurs at Home Bay, also situated along the east coast of Baffin Island adjacent to a large shallow shelf with a sharp shelf break (Fig. 1).

Ocean and ice dynamics in the Arctic are likely responsible for considerable variability in the temporal and spatial availability of feeding habitat and cover from predators. The early spring polynyas that are exploited by bowheads are reasonably predictable and presumably important in bowhead foraging ecology (Stirling 1997). The autumn use of Isabella Bay is also clearly documented as an important habitat of recurring use. However, the location and extent of important habitat in other areas or times of the year is more difficult to identify in specific geographic terms. Known bowhead distribution patterns suggest that influential habitat features may include: (1) ice characteristics such as concentration, age or thickness, and floe size, (2) bathymetry or bottom slope, (3) oceanographic features that concentrate prey such as troughs, upwellings, eddies, funnelling ocean currents and water mass boundaries, and (4) landscape patterns that provide cover from killer whales or reduce the likelihood of killer whale occurrence. For the latter, winter habitat may be characterized by sea ice features that provide habitat that excludes killer whales while minimizing the risk of ice entrapment. Over wintering habitat is thus likely important for protection from predators and is coincident with the period of mating.

Sea ice features that characterize bowhead habitat use

The quantity of ice cover is highly dependent on environmental conditions (Johannessen et al. 2004). The predicted reduction of available ice due to climate change will likely effect bowheads negatively by reducing the availability of sea ice habitat.

Nursery areas, such as northern Foxe Basin, are characterized by shallow waters and ice cover, providing safe and relatively calm waters with simple predictable oceanographic processes suitable for nursing newborns during spring and early summer. As the season advances toward the annual ice minimum, increased vulnerability to predation likely occurs, as killer whales are physically or behaviourally able to navigate more open-water conditions. Extensive ice cover in Prince Regent Inlet and the Gulf of Boothia regions, which persists during most summers, provides nursery habitat throughout the summer and fall period.

Killer whales in the Canadian Arctic sometimes hunt along ice edges and leads but typically avoid heavy ice concentrations (Reeves and Mitchell 1988, Higdon 2007), presumably because of their dorsal fin or due to a behavioural tradition. Thus, for bowheads 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 or shallow waters also provides opportunity for prolonged and undisturbed social encounters such as mating (Finley et al. 1993). Estimation of the likelihood and impact of predation with varying temporal and spatial ice conditions that include forecasted sea ice reductions in ice extent and thickness is necessary research required to better understand bowhead habitat use.

Polynyas are annual open-water events occurring during the ice seasons that provide productive areas for foraging while offering suitable protection from predation of young animals. Through direct solar radiation on open water and upwelling of nutrients due to wind and water currents, polynyas produce early summer primary and secondary production blooms, creating optimal habitat for intensive bowhead foraging to replenish energy stores diminished over winter. Variation in the magnitude of the primary and secondary productivity and in the predictability of spatial and temporal occurrence of these polynyas, as determined by annual environmental variation, likely affects the extent and importance of polynya food resources for whales. However, it is not known what proportion of bowhead annual diet is obtained from these habitats, nor to what extent the availability of resources from this source varies temporally or spatially.

Geographic features that characterize bowhead habitat use

Complex coastal areas offer bowhead habitat that provides calm waters suitable for young animals and social interaction for adults as well as providing suitable cover from killer whale predation in the absence of ice. Cumberland Sound and Frobisher Bay, off southeast Baffin Island (Fig. 1), may be used, at least seasonally, for this purpose. Complex geography and bathymetry may provide for acoustical refuge from killer whale sonar and thereby mask bowhead sounds that may indicate prey presence. The presence of killer whales is well known to drive marine mammals close to shore in open water habitat (Frost et al. 1992, NWMB 2000, Gonzales 2001). Evidence for this behavioural response includes the occurrence of an Inuktitut word for “fear of killer whales”, which is called ‘*aarlungajut*’ translated as a fear reaction to the presence of *aarluit* or killer whales (NWMB 2000).

Complex landscape areas likely also provide many physical features that enhance opportunities for intensive foraging, as illustrated by the well documented behaviour of bowhead feeding in troughs during fall in Isabella Bay (Finley 1990, Finley *et al.* 1993) on eastern Baffin Island (Fig. 3). In the summering complex of Prince Regent Inlet/Gulf of Boothia, bowheads move closer to shore during the summer and fall period, and move into Bernier Bay, Lord Mayor Bay and Pelly Bay (DFO unpublished data). The extent and variability of food production, feeding, and protection from predation in this habitat has not been quantified.

Fury and Hecla Strait is a narrow channel used by a segment of bowhead population in spring and fall to move between the spring “nursery” area of northern Foxe Basin and the summering complex of Prince Regent Inlet/Gulf of Boothia. Historically, presence of continuous ice cover in the Strait may have restricted movements of whales into Prince Regent Inlet in most years. However, in recent years the Strait has not restricted movement (also see Higdon and Ferguson *In press*). The risk of ice blockage may actually increase in the short term with climate warming as Arctic Ocean and Canadian Archipelago multi-year ice breaks up and makes its way through channels towards the Atlantic Oceans (Mundy and Barber 2001).

Whales use spring ice leads as they move from areas of diminishing ice in late winter to ice-surrounded polynyas in spring. Important ice leads used by bowheads include the continental shelf break off northern Baffin Bay, along eastern Baffin Island, from Hudson Strait to northwestern Hudson Bay and northern Foxe Basin, and from northern Foxe Basin to Gulf of Boothia and Prince Regent Inlet.

METHODS

Bowhead Tagging

Research into bowhead whale movements in Canada was conducted from 2001 to 2006 in northern Foxe Basin (July 2002 and 2003) and in Cumberland Sound (May 2004 and July 2005-2006). Movements of 14 whales were recorded using satellite-linked telemetry consisting of SPOT (position only) tags and SDR (dive-recording) tags. SPOT tags were manufactured by Wildlife Computers (Redmond, Washington) whereas the SDR transmitter was a model “SDR T-16”, supplied by Telonics and modified by Wildlife Computers. Both the SPOT and SDR tag transmitters provided information on date, time, and location of the whale, as well as information on the quality of location estimates (Heide Jørgensen *et al.* 2006). See Dueck et al. (2006) for deployment details.

Analysis of Argos Data and Utilization Distribution Estimation

To ensure validation, Argos locations were filtered first manually to remove erroneous outliers (Dueck et al. 2006) and then subsequently checked using the McConnell et al. (1992) iterative forward/backward averaging filter which used Advanced Research Global

Observation Satellite (Argos) location quality and estimates of the likely velocity of bowhead whales (Fig 4).

We used density of PTT tracking data to identify areas of high use by bowhead whales. For locations less than 24 hours apart, the path of the whale was interpolated at hourly intervals. If the interval between uplinks was more than 24 hours, paths were not interpolated. Thus, the interpolation method ensured that each trip was weighted by its duration in calculating density distributions.

Kernel density estimators have been shown to be useful to quantify habitat use and estimate home ranges (Matthiopoulous 2003). Here, we used kernel density to identify core areas of utilization for conservation and therefore chose a coarse 0.5 degree grid square as the smoothing (or *h*) parameter (see BirdLife International 2004). Although a 0.5 degree smoothing parameter causes the shape of the kernel to vary with latitude, we considered this change small in relation to the scales of bowhead habitat use.

The density grids derived from kernel analysis for each whale was adjusted according to the number of interpolated PTT locations for the dataset and then weighted by the number of individual whales tagged and at sea. The density distributions are represented on maps by Utilization Distributions (UD) that provide probability contours indicating the relative time whales spend in particular areas (Pinaud and Weimerskirch 2007). For example, a 50% UD contour represents the area where tagged whales spent 50% of their time.

Defining seasons

First, we adjusted all distances according to the time between locations to remove the fractal effect of varying time between locations (Ferguson et al. 1998). Next, the residuals of the log-linear regression were used in a polynomial regression against Julian day. To assess the best fit model of the 12 polynomial regressions we used Akaike's Information Criterion (AIC; Burnham and Anderson 1998). Movement seasons were delineated by the inflection point indicative of a change in movement rate (km/day) from increasing to decreasing or from decreasing to increasing and thereby demarcated the beginning or end of seasons (Ferguson, 2002; Ferguson and Elkie 2004).

Distance moved was non-linearly related to days between telemetry locations. To control for this effect, we used residuals from the log-log linear regression against Julian day. Fitted polynomial regressions, assessed according to AIC, determined that the best fit was a 4^{th} order polynomial that described 2 seasons (data on file). The first season, defined as “summer” was 184 days long, lasted from 27 June – 27 December, and was characterized by high rates of movement (31.9±1.05 km/d, n=970). In contrast, “winter” lasted 78 days, occurred from 28 December – 15 March, and was characterized by low movement rates (16.6±2.65 km/d, n=153). The remaining “spring” period (16 March – 26 June) was not adequately sampled by the available data, limiting results outlined below. There was some evidence of two migratory periods, indicated by peaks in movement rate, that occurred on 22 July when whales were moving to summer range and on 29 October when whales were returning to winter range. A small peak of movement occurred by 3 April that may reflect when whales travelled to spring range. However, the reduced sampling available for analyses in spring provided minimal seasonal habitat use information from the spring Utilization Distribution map.

RESULTS AND DISCUSSION

Seasonal bowhead habitat use

Bowhead whales range annually over much of the eastern Arctic (Fig. 1). The historic range extended along the Labrador coast; although this area is not thought to be highly used by bowhead whales at present, it may provide suitable habitat for an expanding bowhead whale population (Jacques Whitford–AXYS 2007). Temporal use of particular habitats (described below) occurs for varying periods and is largely derived from the Utilization Distribution maps of 14 whales tagged with satellite transmitters. Figure 5 shows the annual occupancy of use by these whales and is limited by tagging location and tag longevity, since whales tagged in Greenland appear to constitute another component of the population with movements and seasonal distribution not completely documented by these whales (Heide Jorgensen *et al.* 2007).

Wintering habitat

Wintering areas occur in Hudson Strait and the pack ice of Davis Strait (Reeves *et al.* 1983, Turl 1987, Dueck *et al.* 2006, Koski *et al.* 2006). Wintering areas are characterized by ice cover in association with sufficient open water access, providing protection from predators generally and more specifically during calving, while minimizing ice entrapment. Concentrating whales into the small areas providing these particular ice characteristics may shape mating behaviour. Conversely, changing ice conditions that open up more winter habitat may predispose whales to environmental features unique and non-adaptive to their evolved mating behaviour. Wintering habitat is found in Hudson Strait, the mouth of Cumberland Sound, and the ice margin of Davis Strait between Canada and Greenland (Dueck *et al.* 2006, Heide Jorgensen *et al.* 2007, Turl 1987), as well as Frobisher Bay as shown in Figure 6. The largest proportion of the population appears to winter in Hudson Strait (Koski *et al.* 2007).

With the advancing spring season and start of the ice break up, the protective characteristics offered by winter habitat diminish and with open water, whales move northeast and northwest in advance of the receding ice. Loss of preferred winter habitat may result in increased risk of ice entrapment and/or increased risk of predation, and potential disruption of mating if the opposite sexes have difficulty finding each other. Quantification of the effects of winter habitat loss is not possible at present.

Spring habitat

In early spring, a segment of the bowhead population not represented in the Utilization Distribution map (Fig. 7) travels to the western coast of Greenland to Disko Bay (Eschricht and Reinhardt 1866, Heide-Jorgensen *et al.* 2003). The whales tagged in spring from Cumberland Sound and northern Foxe Basin includes whales that leave the wintering grounds and travel along the east coast of Baffin Island and/or move west through Hudson Strait to polynyas in northwestern Hudson Bay and northern Foxe Basin (Reeves *et al.* 1983, Dueck *et al.* 2006).

During spring, areas of open water surrounded by ice cover, and the initiation of primary productivity, provides both seasonal food availability and protection from predators. However, considerable annual environmental variability affects the timing and extent of productivity in Disko Bay, North Water polynya, northern Foxe Basin, and northwestern

Hudson Bay. Loss of spring habitat in one or more of these areas is likely to reduce foraging opportunities and/or safe refuge for a component of the population. With continued population growth the risk associated with loss of spring habitat will increase as this may be a limiting season for population demography and associated density-dependent effects (e.g., Clutton-Brock et al. 1987).

Northern Foxe Basin is considered particularly important for calves and juveniles as a nursery area (Finley 2001) and thus spring habitat is critical to survival and reproduction and overall population health. Quantification of the effects of spring habitat loss is considered a high priority for future research needs.

<u>Summer-fall habitat</u>

During summer as the extent of sea ice is reduced, one segment of the bowhead population continues to move further into the archipelago (Dueck *et al.* 2006) whereas another segment of the population remains along the coast of eastern Baffin Island (Finley et al. 1993, Heide-Jorgensen *et al.* 2003). Figure 8 describes the distribution of tagged whales during this season, excluding whales from the West Greenland segment of the population. The summer movement peaks on 22 July, bringing whales to the Prince Regent Inlet/Gulf of Boothia summering area. The fall migrations southward peak on 29 October, bringing whales towards the wintering grounds along the east Baffin Island coast as well as through Fury and Hecla Strait and Foxe Basin.

During the summer, the Prince Regent Inlet/Gulf of Boothia summering area provides the largest ice covered area remaining within the range of eastern Arctic bowheads (Fig. 3). Known to whalers as the “nursery”, it is the refuge for juveniles and adult females with young (Finley 1990). In addition to relatively predictable ice cover, the region contains a number of features that may increase prey availability and accessibility through oceanographic processes that concentrate prey. These features include the large scale current within the basin that feeds ice and Pacific water nutrients into the complex originating from the Arctic Archipelago. Creswell Bay and Bellot Strait probably contribute significantly to primary production by providing nutrient-laden and Pacific waters respectively. Interacting currents, eddies and upwellings within the complex are likely important features that provide bowhead feeding opportunities throughout the summer and early fall. In late summer, many satellite-tagged bowheads moved into the complex coastal area of Lord Mayor Bay and Pelly Bay whereas in years of ice minima, bowheads used Elwin Bay and Committee Bay (Dueck et al. 2006).

The spatial extent of the summering area is much greater than for other seasons and considered more dynamic temporally within areas. At the same time, less is known about foraging ecology of bowhead whales generally and specifically for eastern Arctic bowheads while on their summer range. Annual variability in the Arctic environment and its subsequent effects on foraging habitat is likely greatest during the open-water season. Some mechanisms that function to concentrate bowhead prey, such as shelf breaks, may be quasi-permanent while others are transient and less predictable, such as currents and winds. Loss of traditional summering habitat as a result of global warming may result in bowheads travelling over large distances to new areas, thereby limiting foraging opportunities, or increasing the energetic cost associated with greater movement, or displacing animals to habitats that result in greater vulnerability to predation.

Bowheads are believed to feed intensively during fall, replenishing much of their energy stores during this period (Finley 2001). We speculate that bowhead whales congregate spatially along upwelling fronts and temporally during fall (September through November). Key upwelling events likely co-occur with whale spatial congregation during fall in Prince Regent Inlet and western Baffin Bay, as exemplified by the aggregation of whales at Isabella Bay (Finley 1990, Finley *et al.* 1993).

Oceanographic processes appear to concentrate bowhead prey both temporally and spatially (Toda 2005). Along the east coast of Baffin Island, numerous fjords are associated with troughs extending out to the continental shelf. Cold deep water current is generally northwest along the Baffin Island coastline consisting of both Pacific (Lancaster Sound) and Atlantic (Nares Strait) cold salty water. The late open-water season is also well-noted for the development of strong winds. During southeast winds, surface water is moved in the opposite direction of the underlying cold water current causing upwelling events along the north side of fjord troughs. Such events occur due to surface water moving along the shelf drawing deep nutrient-rich Pacific/Atlantic water to the surface at the trough and continental edge. These waters warm as they are brought to the surface and become available for a phytoplankton bloom during the early open-water season. During the late open-water season, after feeding on the phytoplankton, zooplankton dramatically increases in numbers (Scott et al. 2000, McLaren et al. 2001). Increased copepod density and food quality (i.e., lipid-rich during autumn; Falk-Petersen et al. 1987) at a topographically-determined upwelling site causes a concentration of bowhead prey at the upwelling site. Also, when wind patterns are reversed a down-welling can occur which can still function to concentrate prey as zooplankton swim to the surface to avoid being drawn to deep water and as a result become concentrated at the down welling front (Irigoien et al. 2004).

The spatial extent and temporal variability of food production and prey concentrating mechanisms during these intensive feeding periods is not well known. There likely are other areas along eastern Baffin Island (Jacques Whitford–AXYS 2007), or in the Prince Regent Inlet/Gulf of Boothia complex that provide similar physical concentrating mechanisms similar to that found at Isabella Bay. Finley (1990) suggests that although other feeding habitat along east Baffin Island may exist, known areas such as Isabella Bay may represent important, unique and limited habitat.

Threats that characterize bowhead habitat use

We consider two categories of threats to bowhead habitat. First, with continued global warming and loss of sea ice thickness, extent, and duration requires consideration of migration routes, travel corridors, and use of sea ice associated with feeding areas and refuge from predation. Second, with a longer open water season increased use of the Arctic for exploration, development, tourism, human habitation, and travel will result in greater ship traffic and associated anthropogenically derived noise.

Change and/or loss of habitat along migration routes between overwintering areas, spring areas and summering areas could redirect animals from their preferred route, resulting in energy losses, increased risk of predation, or lack of access to areas critical to life processes such as calf rearing and feeding. For example, Fury and Hecla Strait is a narrow channel used by bowheads in northern Foxe Basin to reach the Prince Regent Inlet/Gulf of Boothia complex. Blockage of this channel due to movement of multi-year ice during July and early August (spring migration), or alternatively during September to late

October/early November (fall migration) could strand individuals in unsuitable foraging habitat, and either increase the risk of predation or increase the risk of ice entrapment. With decreasing sea ice during summer, distances between wintering and summer areas may increase, resulting in longer and more energetically expensive migrations.

Climate change is likely to alter the quantity and quality of particular habitats and create contrary effects to eastern Arctic bowhead population viability. For example, continued loss of annual sea ice will likely result in an extension of bowhead habitat farther into the Archipelago while providing the opportunity for other competing whale species to extend their geographic range into areas currently used by bowhead whales. Positive effects may include greater food availability as primary productivity increases with warmer temperatures and negative effects may include year-round risk of predation due to loss of sea ice as a predator refuge. However, the overall prediction is for the requisite Arctic sea ice habitat used by bowheads to eventually become limited as remaining sea diminishes towards the pole. 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.

Global warming has the potential to affect bowhead calving, migration, feeding, and use of over-wintering range. We speculate that bowhead calving grounds can be considered "traditional" and are likely behaviourally rigid. If this conjecture is reasonable then an expectation is that with loss of sea ice these traditional areas that offer reduced risk of killer whale predation, particularly to smaller juveniles, will become used by killer whales, a more behaviourally flexible and opportunistic predator, resulting in greater calf mortality. Feeding areas are probably more flexible and bowheads will be able to accommodate changes in distribution of feeding sites with loss of sea ice through greater wandering and exploratory behaviour. However, traditional migration corridors and possible staging grounds may become less useful relative to their original purpose (e.g., safe movement and brief feeding). Over-winter habitat is also a critical sea ice process required for bowheads to minimize predation and ice entrapment while awaiting spring break-up and accessibility to feeding areas. With loss of sea ice the location of winter areas may change their spatial distribution considerably.

There is no evidence presently that suitable habitat for bowhead whales is a limiting factor to the recovery of bowheads in the eastern Arctic. However, one hypothesis is that the Newfoundland-Labrador niche vacated by the loss of large numbers of bowhead whales to commercial whaling may have been filled by competing rorqual whales and other animals, such as harp seals (*Phoca groenlandica*), capable of exploiting the same zooplankton prey base. Similar explanations have been made for Antarctic rorqual populations that have not recovered to pre-commercial densities (Stachowitsch 2003). If this scenario is credible, then the prediction for loss of subpolar habitat with climate warming may result in altering bowhead habitat in the long-term and thus, the ability of bowheads to recover to spatially-specific established recovery targets may not be viable.

With loss of sea ice in the Arctic, predictions are for greater human activities that include seismic exploration and ship traffic. Ship traffic may displace bowheads from preferred migration routes or from areas of preferred seasonal habitat. Ship strikes may lead to injury or death of individuals. Also, bowhead whales use sound to communicate and for navigation. Airguns used in seismic surveys generate sound at frequencies that coincide with hearing ranges used by whales and dolphins and thus acoustic disturbance has the potential to cause whale displacement due or interference with whale behaviour, such as feeding, social interactions (including breeding) and navigation, as well as having the potential to cause physical harm (Richardson et al. 1986). Avoidance of noise as a result of seismic activity may alter local movements and migration patterns, inhibiting typical seasonal patterns with concomitant negative effects.

Due to their large size, bowhead whales travel great distances, occupy expansive home ranges, and use different habitat features at different times of the year. Caution is necessary in allocation decisions to ensure that critical habitat of one kind is not altered or disturbed on the premise of the existence of other critical habitats that serve a different seasonal function. Last, cumulative effects that combine climate change/sea ice and killer whales, or ship strikes and increased ocean noise into non-additive effects could adversely affect bowheads in ways yet to be determined.

CONCLUSIONS

In our review, we have considered two approaches that incorporate important bowhead habitat selection process: energy acquisition in support of reproduction and early age survival and avoidance of mortality risk factors.

Bottom-up processes relate to how energy acquisition may affect reproduction and growth of whales. Here, energy acquisition is manifested as changes in life-history parameters, in particular age at maturity, interbirth interval, and juvenile survival. We suggest that to acquire sufficient knowledge of bottom-up processes on bowhead population demography requires conservation research that answers the following five questions. What is the major food group? What is the major season affording the greatest intake of energy? Where and in what habitat does the major foraging activity occur? What is the distribution of oceanographic features associated with foraging areas? And finally, how will these key habitat features be temporally and spatially affected by major environmental changes such as climate warming and anthropogenic activity? Thus, it is necessary to forecast changes using climate models to anticipate change and thereby provide the opportunity to mitigate. Also needed are models of energetic requirements of bowhead energy acquisition (feeding ecology), fat storage, movement costs, and forecast energetics relative to changes with future predicted sea ice with polar warming.

The second part is to understand bowhead “critical” habitat processes. This requires study of top-down processes that affect how mortality affects bowhead population growth. There are two questions that need to be answered. Firstly, what are the sea ice conditions in winter that provide reduced risk of ice entrapment? Here, cartographic methods would define winter sea ice condition requirements and model scenarios of changes in winter ice with climate change predictions to understand where winter areas will occur in future. Secondly, what are the movement and habitat requirements for bowheads to reduce risk of killer whale predation? Here, research is needed to understand the function of calving areas and how these can change in space and time associated with climate change models. Together, understanding the top-down and bottom-up processes involved in bowhead population regulation will afford a conservation plan that includes the identification of critical processes and their geographic locations with change.

In summary, known Bowhead distribution patterns suggest that influential habitat features may include the presence of four main environmental features: suitable ice cover to reduce predation; proximity to shallow bathymetry or bottom slope for nursery functions;

oceanographic features that concentrate prey (e.g., troughs, upwellings, eddies, funneling ocean currents, and water mass boundaries); and complex coastal areas that provide cover from predation, calm waters, and enhanced opportunities for intensive foraging. Our review of bowhead habitat use suggests the Eastern Arctic Bowhead Recovery Team should consider the following habitat processes and current use areas in its assessment of critical habitat: (1) overwinter habitat in Hudson Strait and Davis Strait to reduce risk associated with ice entrapment and killer whale predation (from about late December to late March); (2) the northern Foxe Basin calving area associated with habitat used to nurture and shelter neonates and juveniles (from about late May to late July); (3) the Gulf of Boothia-Prince Regent Inlet region associated with nursing female bowheads accompanied by calves (from about late July to October); and (4) the mid-eastern coastline waters off Baffin Island where consistent autumn feeding occurs (from about mid-July to late October).

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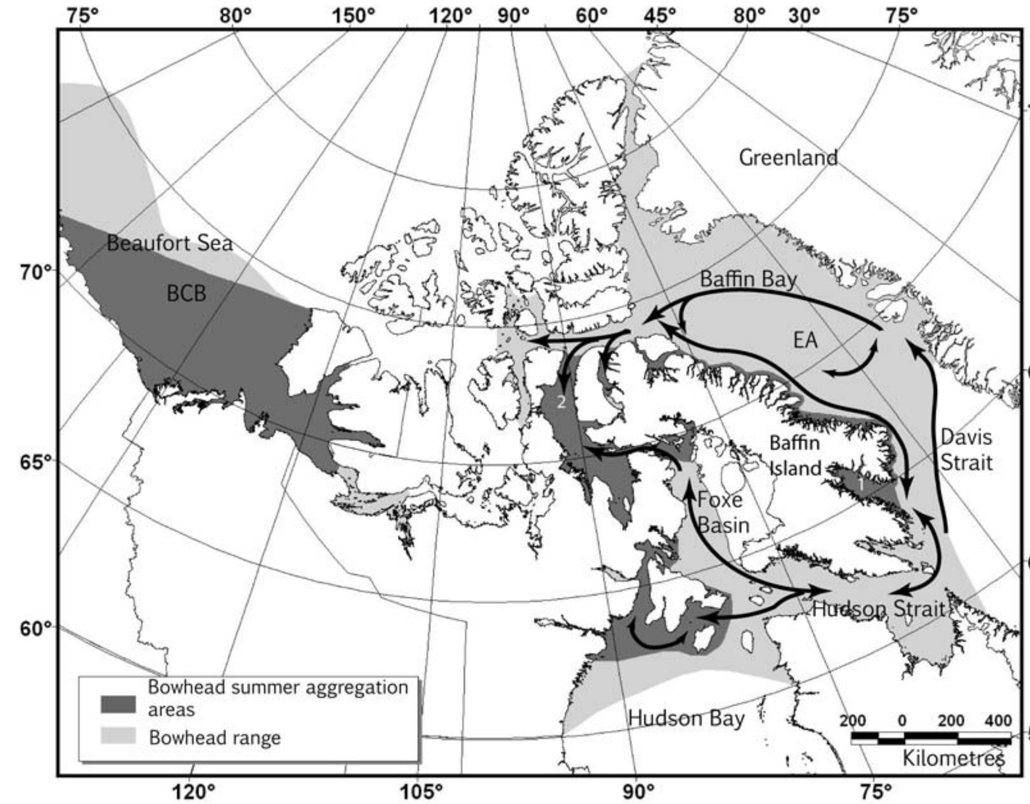

Figure 1. Map depicting the range of bowhead whales in the western and eastern Canadian Arctic, and illustrating the generalized migration routes for the eastern Arctic population. From the wintering areas in the vicinity of Hudson Strait, Cumberland Sound and Davis Strait, whales move toward Greenland, toward northwest Hudson Bay and northern Foxe Basin, and north along the east coast of Baffin Island. From west Greenland, whales continue to spring season areas in northwest Baffin Bay. From northern Foxe Basin whales move into the "nursery" summering area of Prince Regent Inlet and Gulf of Boothia. From northwest Baffin Bay some whales continue into the archipelago while others turn southward along the east coast of Baffin Island.

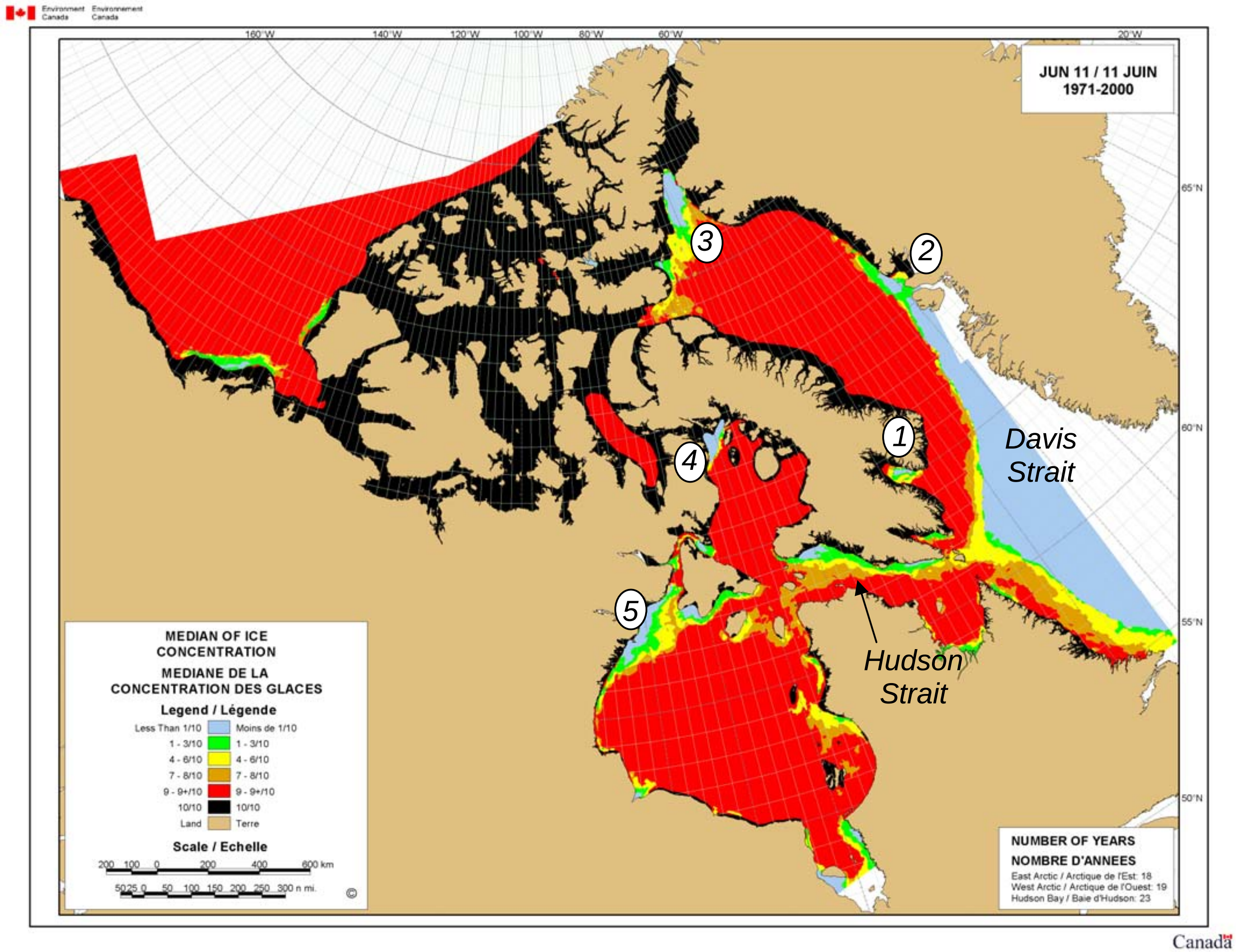

Figure 2. Environment Canada map depicting median ice concentration for the eastern Canadian Arctic for the week of June 11. Note the areas of open water coincident with spring bowhead distribution: Cumberland Sound (1), Disko Bay (2), North Water (3), northern Foxe Basin (4), and northwest Hudson Bay (5).

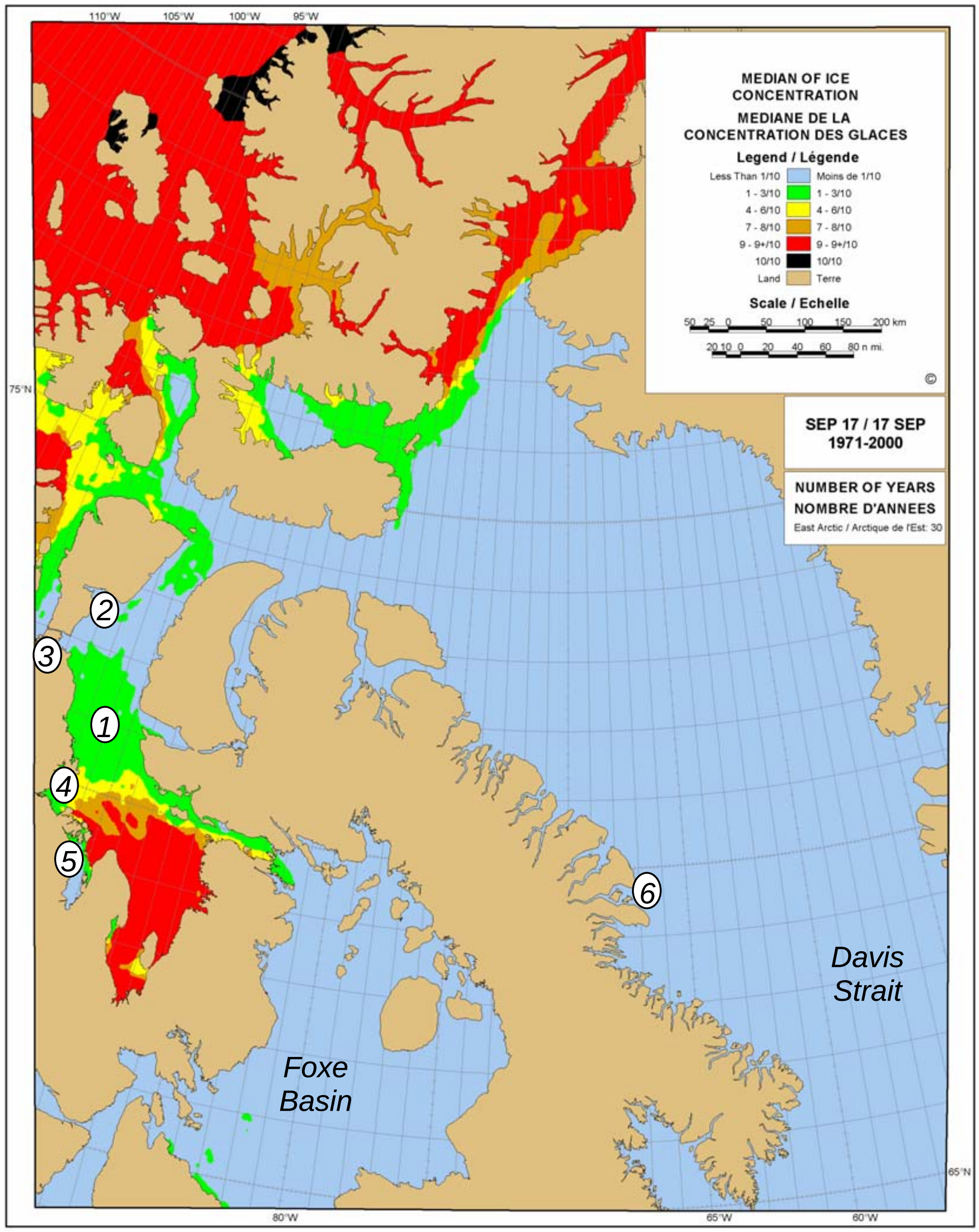

Figure 3. Environment Canada map depicting median location for the annual ice minimum. Note that the Prince Regent Inlet/Gulf of Boothia complex (1) provides the only area of consistent ice cover within the range of eastern Arctic bowheads. This is an important summering area for juveniles and adult females with young. Potentially important features include Creswell Bay (2), Bellot Strait (3), Lord Mayor Bay (4), and northern Pelly Bay (5). An important fall aggregation area exists at Isabella Bay (6).

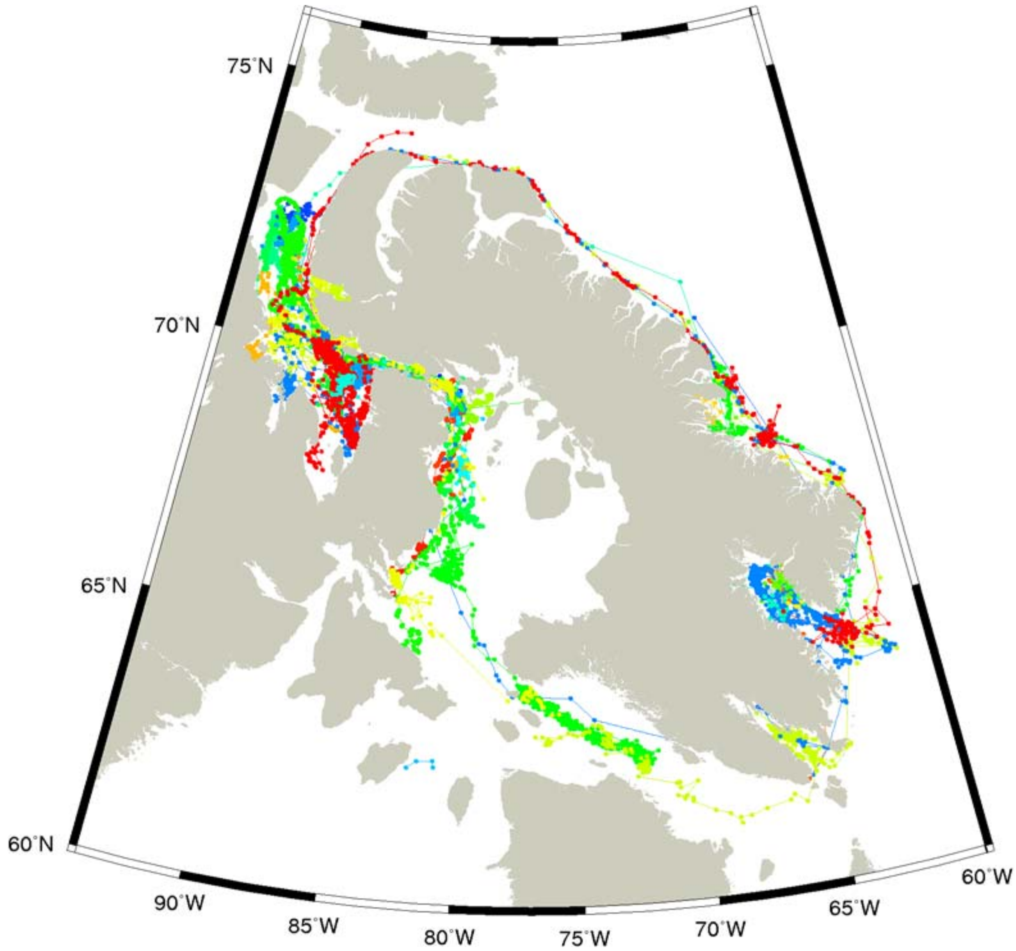

Figure 4. Bowhead whale movement tracks from satellite telemetry locations derived from 6 bowheads tagged in northern Foxe Basin (July 2002 and 2003) and 8 in Cumberland Sound (May 2004 and July 2005-2006). Different whales are indicated by different colours.

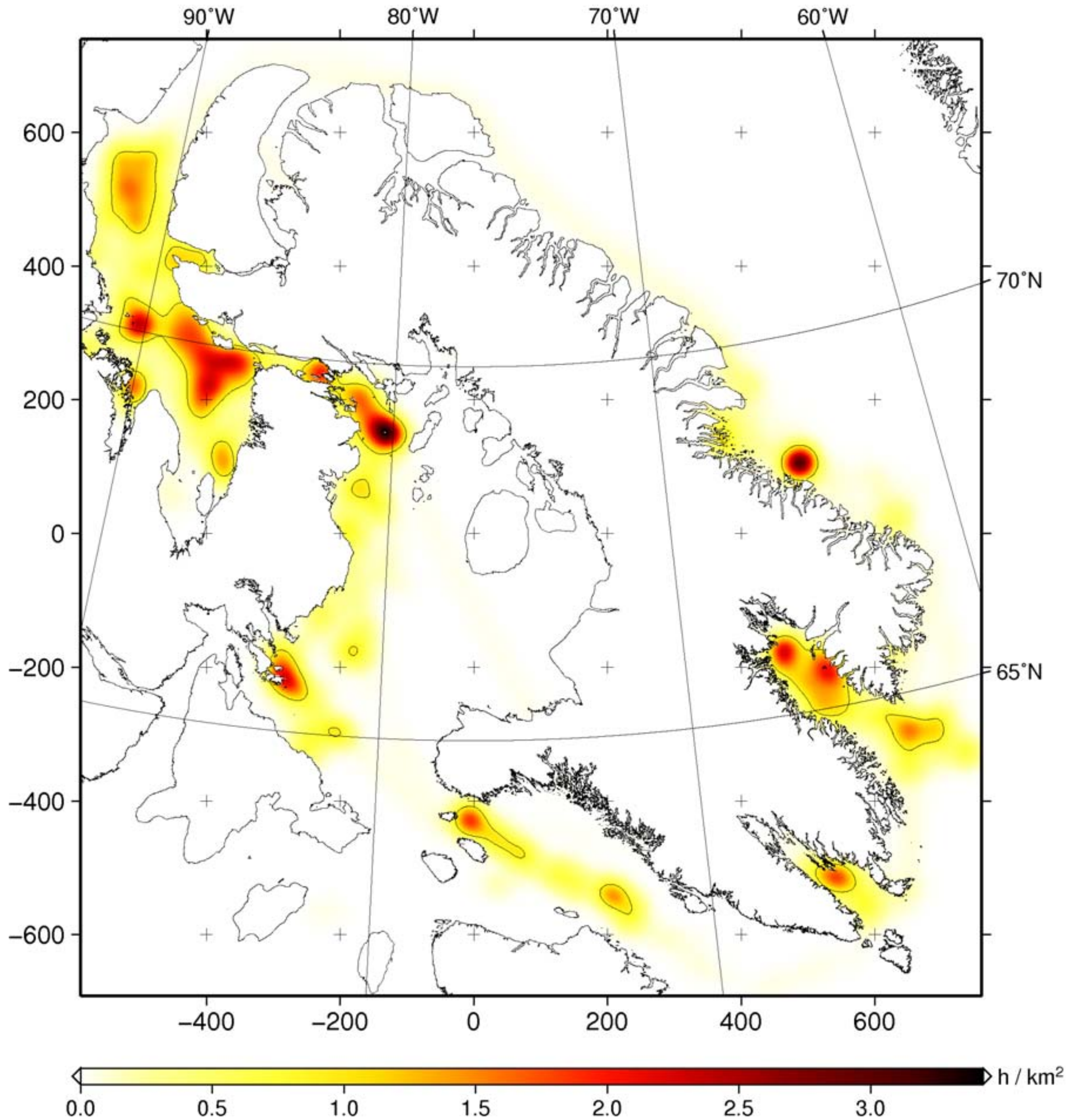

Figure 5. Temporal concentrations of bowhead whale use of the eastern Arctic derived from all satellite telemetry locations of 6 bowheads tagged in northern Foxe Basin (July 2002 and 2003) and 8 in Cumberland Sound (May 2004 and July 2005-2006). Darker colour indicates greater time spent in the area. The map and the following maps likely represent an incomplete assessment of potentially important habitat for this population as variations in habitat use may occur among animals and years, and it does not include data for whales tagged in Greenland.

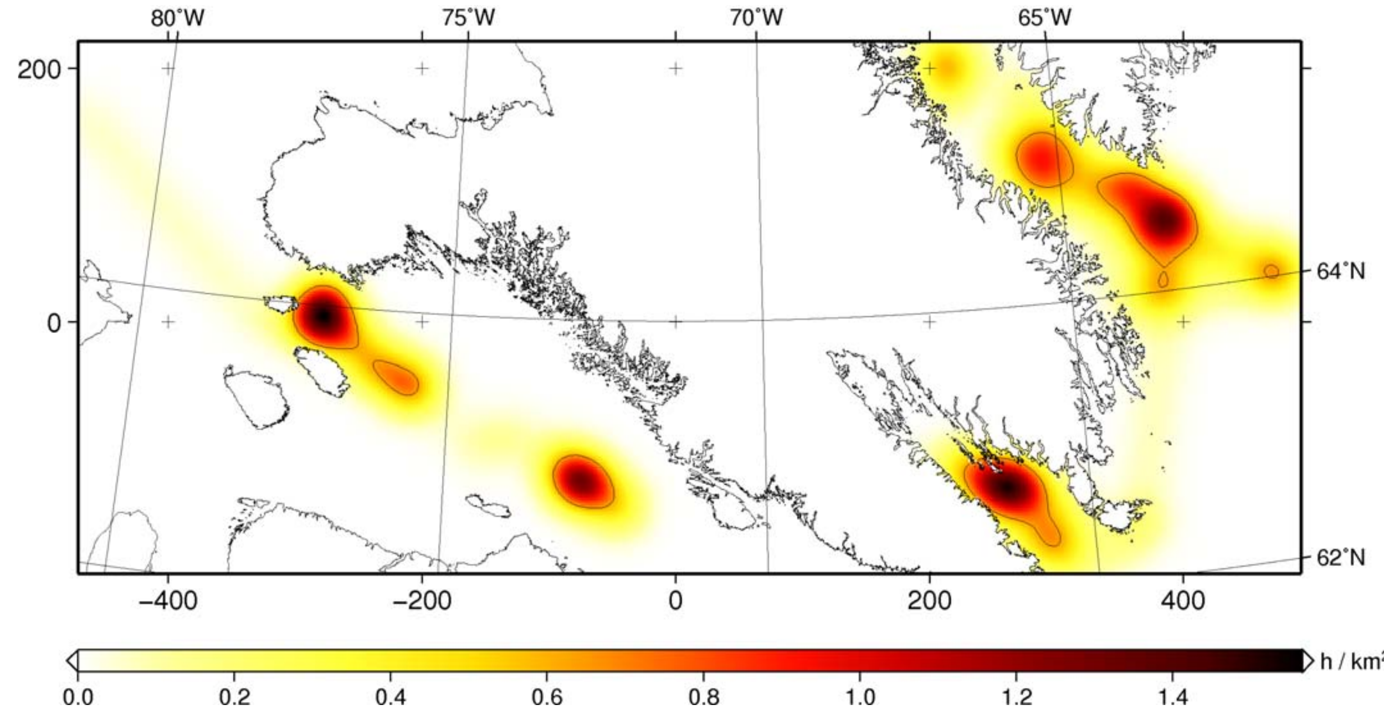

Figure 6. Temporal concentrations of bowhead whale use of the eastern Arctic derived from winter (28 December to 15 March) satellite telemetry locations of 8 bowheads tagged in Cumberland Sound (May 2004 and July 2005-2006).

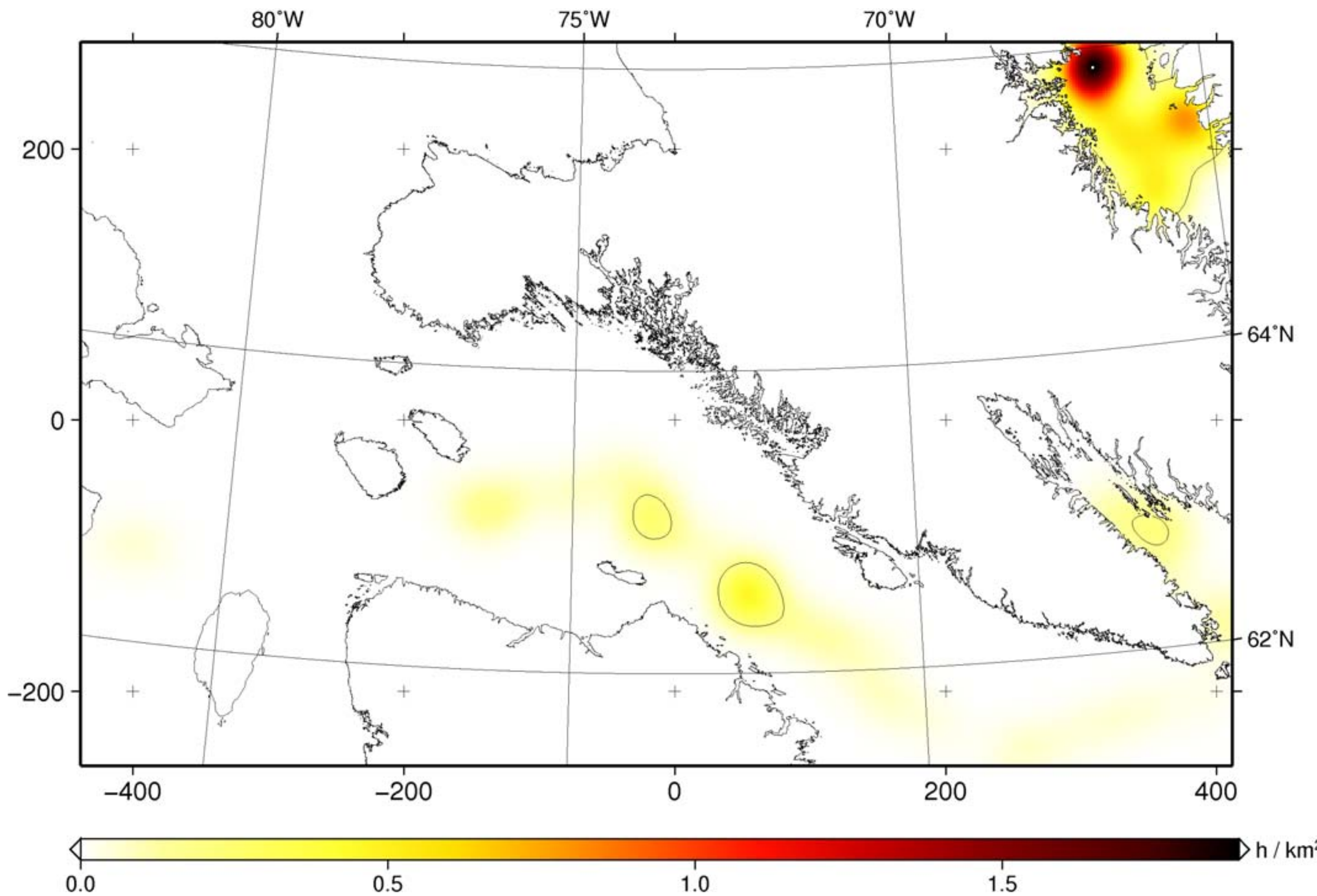

Figure 7. Temporal concentrations of bowhead whale use of the eastern Arctic derived from spring (16 March to 26 June) satellite telemetry locations of 8 bowheads tagged in Cumberland Sound (May 2004 and July 2005-2006).

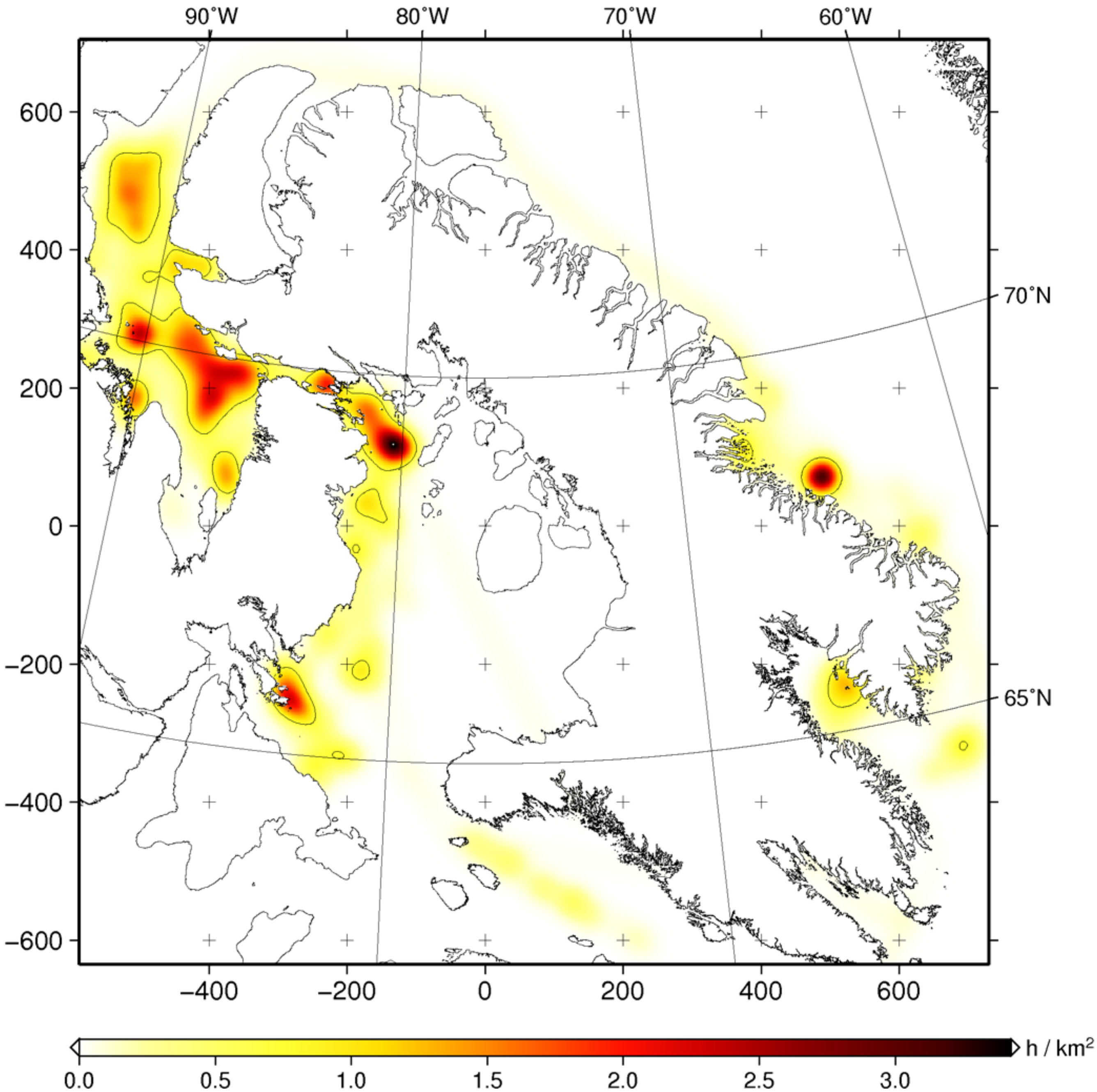

Figure 8. Temporal concentrations of bowhead whale use of the eastern Arctic derived from summer (27 June to 27 December) satellite telemetry locations of 14 bowheads tagged in northern Foxe Basin (July 2002 and 2003) and in Cumberland Sound (May 2004 and July 2005-2006).