SC/67B/AWMP/04

Bering-Chukchi-Beaufort Stock of Bowhead Whales: 20062017 Satellite Telemetry Results with Some Observations on Stock Sub-structure

Lori Quakenbush, John Citta, John C. George,Mads Peter Heide-Jrgensen, Harry Brower, Lois Harwood, Billy Adams, Charles Pokiak, and James Pokiak, Ellen Lea

INTERNATIONAL WHALING COMMISSION

Bering-Chukchi-Beaufort Stock of Bowhead Whales: 2006–2017 Satellite Telemetry Results with Some Observations on Stock Sub-Structure

Lori Quakenbush[1], John Citta[1], John C. George[2], Mads Peter Heide-Jørgensen[3], Harry Brower[4], Lois Harwood[5], Billy Adams[2], Charles Pokiak[6], and James Pokiak[6], Ellen Lea[5]

[1]Alaska Department of Fish and Game, Fairbanks AK, USA, Lori.Quakenbush@alaska.gov
[2]North Slope Borough, Barrow AK, USA; [3]Greenland Institute of Natural Resources, Copenhagen Denmark; [4]Alaska Eskimo Whaling Commission, Barrow AK, USA; [5]Department of Fisheries and Oceans, Canada; [6]Tuktoyaktuk Hunters and Trappers Association, Tuktoyaktuk, Canada.

ABSTRACT
Sixty-four satellite transmitters provided data on bowhead whales from the Bering-Chukchi-Beaufort (BCB) stock between 2006 and 2017 to study their movements and behavior. Sixty-one of which were tagged in the Beaufort Sea and three were tagged in the Bering Sea. In winter, bowhead whales used the western Bering Sea in areas of heavy ice with little use of open water areas. All but one tagged whale migrated past Point Barrow in spring and went to Amundsen Gulf. That whale migrated up the Chukotka coast and summered in the Chukchi Sea. While most whales summered within the Canadian Beaufort Sea, extensive summer movements included travel far to the north and northeast to overlap with bowhead whales from the Baffin Bay-Davis Strait stock. Other summer movements included trips between the Canadian Beaufort and Barrow and back again. One whale, tagged near Point Barrow, traveled to the northern coast of Chukotka, Russia, in the following summer, and did not return to Canada that summer. Fall movements coincided in space and time with oil and gas activities and potentially with shipping activities. Core-use areas that are likely important feeding areas included Amundsen Gulf in spring and summer; Tuktoyaktuk Shelf in summer; Point Barrow in summer and fall; the northern Chukotka coast in fall; and the western Bering Sea in winter. Recent changes in late summer movements (i.e., greater use of mid and western Beaufort Sea) and less use of previous core-use areas in the Bering Sea in winter that were largely ice-free in winter 2016/17 and 2017/18 have occurred and may become more common. None of the movements from tagged whales suggest a multi-stock condition exists within the BCB bowhead whale population.

INTRODUCTION
The Bering-Chukchi-Beaufort (BCB) stock, also known as the Western Arctic stock, is one of five recognized stocks of bowhead whales that occupy Arctic waters (Moore and Reeves 1993). The BCB stock is hunted by indigenous people of Alaska and Russia and is highly valued for food, materials, and cultural significance. Harvest is regulated by a strike quota determined by the International Whaling Commission and locally managed by the Alaska Eskimo Whaling Commission (AEWC). Although the BCB population numbers approximately 17,000 individuals (Givens et al. 2015), the reduction of summer sea ice and other factors associated with climate change (e.g., increased oil and gas activity, shipping, and fishing) require that we know more about BCB movements, important habitats, and behavior in order to best plan shipping lanes and develop effective mitigation measures for industrial activities. A better understanding of movements related to possible stock structure was also an initial objective for tagging bowheads.

In 2005, the Alaska Department of Fish and Game (ADF&G) began a cooperative project (with AEWC, the North Slope Borough, and the Greenland Institute of Natural Resources; funded by Minerals Management Service, now Bureau of Ocean Energy Management) to study the BCB stock of bowhead whales, including their movements and behavior using satellite telemetry. The project expanded to north western Canada in 2007 and the Department of Fisheries and Oceans and Tuktoyaktuk Hunters and Trappers became cooperators. The specific objectives of the project were to work with native subsistence hunters to deploy satellite tags, use satellite telemetry to identify important habitats, and to document the timing and location of movements and behavior relative to industrial activities and physical conditions (e.g., ice, bathymetry, and distance from shore). Before we began this study, general seasonal movements and their timing were best known near the coast and during the whaling seasons. However, little was known about offshore and winter movements (Fig. 1).

Tracking many individual bowhead whales over long distances and time periods (sometimes more than a year) has greatly expanded our knowledge of bowhead range; variability in movements (Citta et al. 2018; Quakenbush and Citta 2018; Quakenbush et al. 2010), summer and fall use areas (Quakenbush and Citta 2018; Harwood et al. 2017; Citta et al. 2015), winter use areas (Citta et al. 2012; Citta et al. 2015); influence of sea ice and physical oceanographic parameters on movements (Citta et al. 2015, Druckenmiller et al. 2017); interaction with disturbances (Quakenbush et al. 2010b) and fisheries (Citta et al. 2014); and evidence of sub-structure in the BCB stock (this paper).

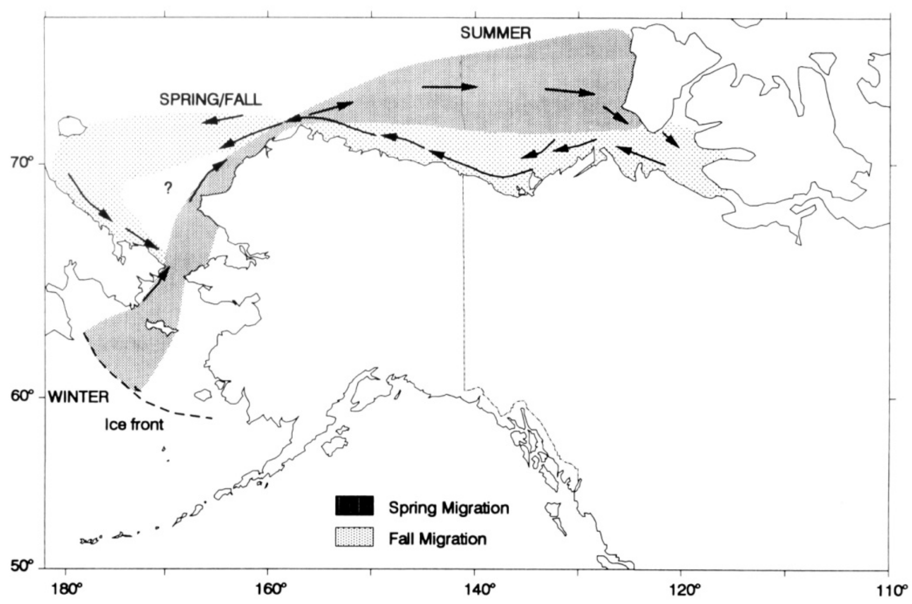

Figure 1. Generalized seasonal occurrence and migration corridor for the BCB bowhead stock prior to 1990, depicting spring and fall pathways (Fig. 9.7, pg 337 from Moore and Reeves (1993)).

METHODS

We used satellite transmitters manufactured by Wildlife Computers (Redmond, Washington, USA) and by the Sea Mammal Research Unit (University of St. Andrews, Scotland) and the attachment and deployment system was developed by the Greenland Institute of Natural Resources (Heide-Jørgensen et al. 2001, 2003; Quakenbush et al. 2010a). Transmitters were placed on bowhead whales in Alaska and Canada in 2006–2017. Most of the tags were deployed by Alaskan and Canadian Native subsistence hunters and boat drivers. Three types of tags were deployed; one that transmitted location only and one that transmitted location and diving information (Quakenbush et al. 2010a), and one that transmitted location, diving, and oceanographic (conductivity and temperature at depth) information. Skin biopsies were collected either by crossbow or by a biopsy rod on the tagging pole. DNA in the skin was used to determine sex of tagged whales (Citta et al. 2012). Transmitter locations acquired from the Argos satellite system were processed using a filter developed by Freitas et al. (2008). Bowhead whale locations that resulted in swim velocities of over 1.94 m/s were removed unless they were within 5 km of the previous location. The threshold velocity of 1.94 m/s is the maximum observed migration speed of bowheads not fleeing vessels or assisted by currents (e.g., Zeh et al., 1993). The filter also has an angular component to account for locations with a high degree of location error that often fall far from the line of travel, forming acute angles between adjacent locations. We used default settings to define the angular components of the filter; within 2.5 km of the track line, locations resulting in angles less than 15˚ were removed and locations between 2.5 and 5 km of the track line were removed if they resulted in angles under 25˚. We then removed locations that fell on land to establish the final set of locations used in our analyses. In order to show areas of concentrated use we used kernel density estimation (Worton 1989, Wand and Jones 1995). Following Quakenbush et al. (2010a), we selected a bandwidth matrix for each whale using Smoothed Cross-Validation (SCV; Duong and Hazelton 2005, Duong 2007).

RESULTS AND DISCUSSION

Sixty-four tags transmitted location and/or dive data between 2006 and 2017. Sixty-one tags were deployed in the Beaufort Sea: 40 tags near Point Barrow, Alaska (6 in the spring, 34 in the fall), and 21 near the Mackenzie River Delta, Canada in the fall. Three tags were deployed from St. Lawrence Island in the spring. Fifteen of the tags transmitted location only and 49 also transmitted dive information. Sex was determined for 41 whales; 14 were females and 27 were males.

Overall Range. This study has extended the boundaries of what was recognized as the range of bowhead whales in every season (compare Figs. 1 and 2). Whales tagged recently are still contributing to the extension of range boundaries indicating that the current boundaries (Fig. 2) will likely be further extended as more whales are tagged. It is unknown whether this range extension is because tagging to date has been insufficient to document the overall range, the increase in population size (Givens et al. 2015) is contributing to an expanded distribution, or if the range is changing as sea ice deceases, or if it is some combination of these. We began to see changes in what we thought was established behavior in the summer of 2016 (e.g., reduced use of the Tuktoyaktuk Shelf summer feeding area and increased use in mid and western Beaufort Sea) and the lack of ice in the primary Bering Sea winter area in the winter of 2016 and 2017 may have altered the wintering area; both may be related to climate change (Quakenbush and Citta 2018) or population increase.

We documented summer (August and September) movements north of Banks Island, Canada, in 2006, and through Prince of Wales Strait into Viscount Melville Sound, Canada, in 2010, a main route of the Northwest Passage. In 2010, a BCB whale left Viscount Melville Sound a few days before a Baffin Bay-Davis Strait stock whale tagged in West Greenland arrived and spent time there in September. Although both whales returned to their respective ranges and did not overlap in time their movements do indicate the two stocks can now intermingle in summer with less ice in the Canadian Arctic archipelago (Heide-Jørgensen et al. 2011; Quakenbush et al. 2012).

Tagged whales moved north of 75 degrees latitude in 2009, 2010, 2012, 2013, 2015, and 2017. These movements occurred north of Banks Island in 2010, north of Wrangel Island in 2009, 2012, 2013, 2015, and 2017, and in the central Beaufort Sea in 2017. Whether bowhead whales have used these offshore areas in summer in the past or if this is recent behavior related to the decrease in sea ice is unknown. The summer and fall range boundary was also extended to the west beyond Wrangel Island in the western Chukchi Sea (Quakenbush et al. 2010; Citta et al. 2018; Quakenbush et al. 2016).

The winter range in the Bering Sea was extended to the east with the movements of a whale tagged in 2012. This whale was included in the analysis to identify primary core-use areas (Citta et al. 2015), but not in the winter movements analysed in Citta et al. (2012 and 2014).

The analysis for spring includes 23 tagged whales that transmitted during the spring migration, and all but one passed Point Barrow and migrated through the Beaufort Sea to Amundsen Gulf, Canada (Quakenbush et al. 2012; Quakenbush and Citta 2018). That one whale (B09-09) migrated a month later than other tagged whales, passing Cape Pe'ek, Russian Federation, on 26 May (Fig. 3) and stayed in the western Chukchi Sea for the summer. This whale was tagged near Point Barrow the previous summer on 29 August 2009, but did not return to Point Barrow the following year, at least through 21 August 2010 when the tag stopped transmitting. We do not know where B09-09 summered prior to being tagged near Point Barrow in 2009. In 2010, we think it unlikely that this whale returned to Point Barrow prior to the fall migration after the tag stopped transmitting. We have some evidence from locating tagged bowheads from the air that they are accompanied by other bowheads (Christman et al. 2013). Thus, we suggest that there may be interannual variation in movements; that is, some whales may not follow the same migration routes each spring or return to the same areas each year and not all bowheads summer in the Beaufort Sea every year as suggested by observations made along the Chukotka coast in summer (Melnikov and Zeh 2007).

That bowheads occur in the western Chukchi in spring is not new. In 2001, Melnikov and Zeh (2007) counted 470 (95% CL 332 to 665) bowhead whales passing Cape Pe'ek, near Uelen, Russia (Fig. 3), between 23 May and 14 June. The spring migration past Point Barrow was believed to be over by 7 June 2001 (George et al., 2004). Based upon travel velocities observed by Melnikov and Zeh (2007), few of the whales observed at Pe'ek in June could have migrated past Point Barrow before 7 June. As such, Melnikov and Zeh (2007) suspected that the whales they observed were remaining in the Chukchi Sea for the summer. Based upon the movements of B09-09, it is clear that some whales do not migrate past Point Barrow every year in spring and that spring migration counts near Barrow (e.g., Zeh et al. 1993, George et al. 2004) do not count the entire BCB stock.

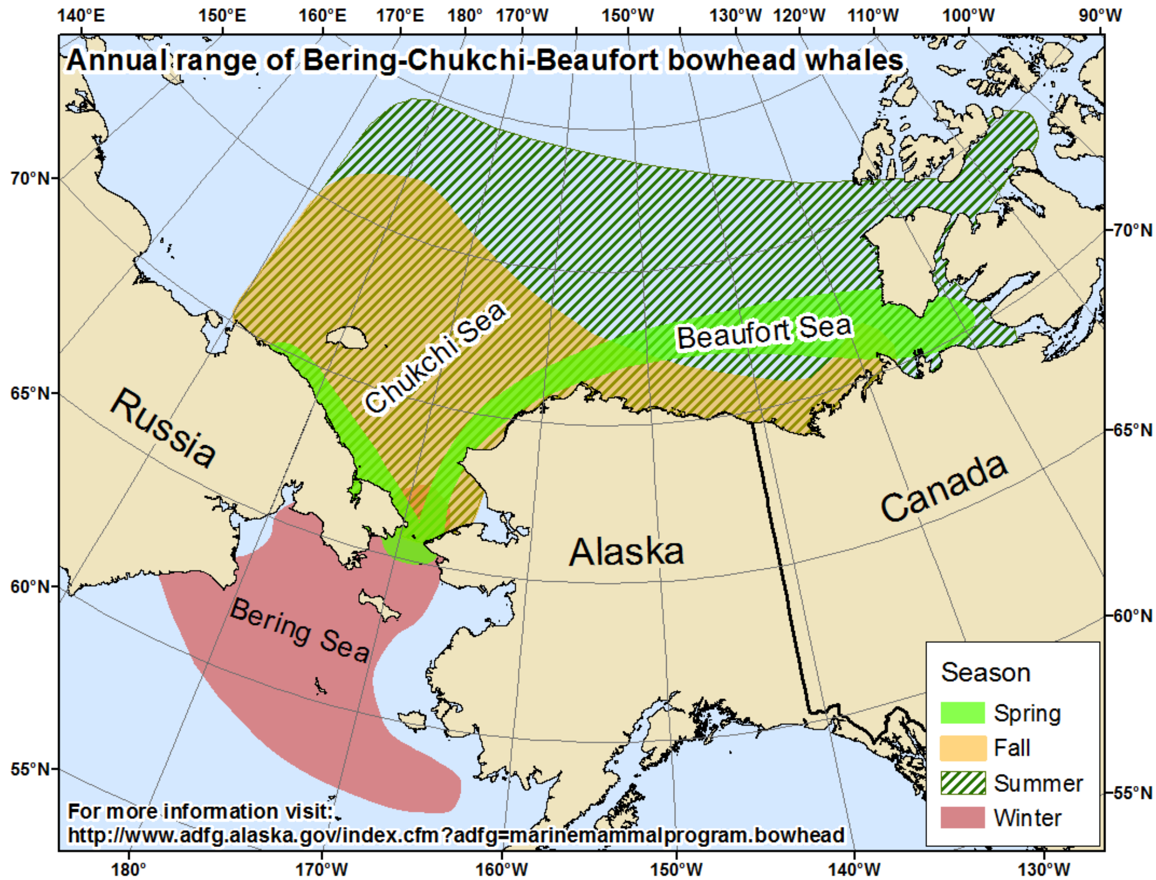

Figure 2. Generalized annual range of the Bering-Chukchi-Beaufort stock of bowhead whales by season from satellite tracking data collected 2006–2017.

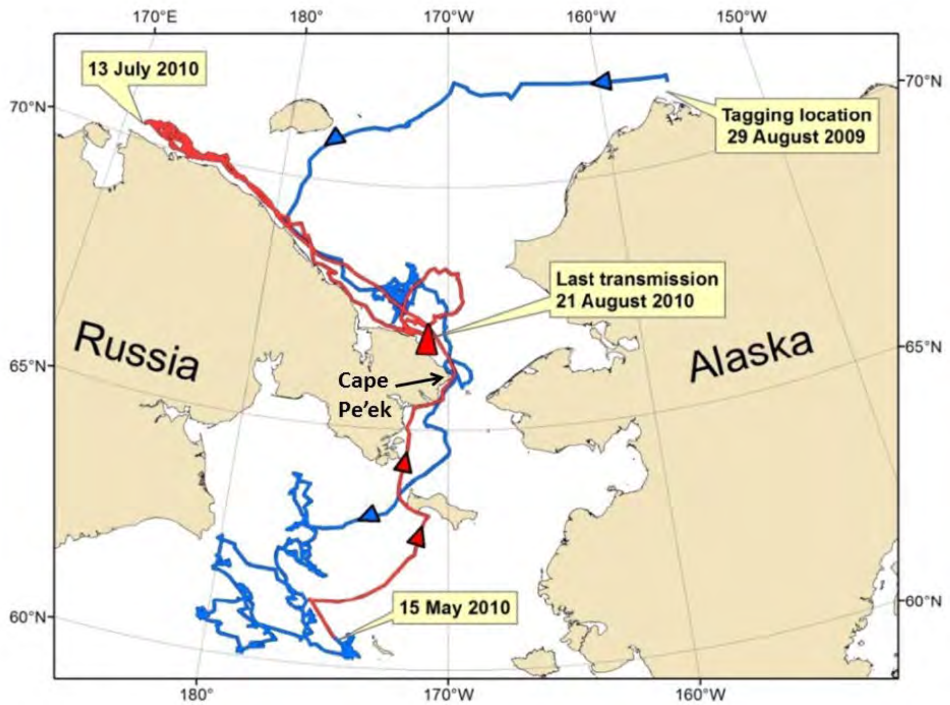

Figure 3. Complete track of B09-09 the only tagged whale of 23 that did not pass Point Barrow in the spring for the Canadian Beaufort Sea but spent spring and summer in the Chukchi Sea. Blue track is 29 August 2009–15 May 2010. Red track is 16 May–29 August 2010.

Feeding Areas. The six primary core-use areas identified in Citta et al. (2015) are believed to be feeding areas that develop seasonally when physical characteristics (oceanography, sea ice, and winds) concentrate zooplankton in areas accessible to bowheads.

In spring, most bowheads leave the wintering area in the Bering Sea and migrate to the Cape Bathurst polynya, Canada (Area 1 in Citta et al. 2015; Fig. 4 below). Here bowheads spent the most time at depths of <75 m within a halocline in the euphotic zone where calanoid copepods are expected to ascend from depths after the winter diapause. Use of the polynya included early May–early July. Whales generally left this area in July when copepods are expected to descend to deeper depths.

During summer and fall (mid-July–late September), most whales moved to the shallow Tuktoyaktuk shelf (Area 2) where favorable (east) winds promote upwelling of copepods onto the shelf where they are concentrated in the shallow water. Whales also concentrated near Point Barrow (Area 3) between late August and early November where east winds also promote upwelling of zooplankton onto the Beaufort Shelf (Fig. 4).

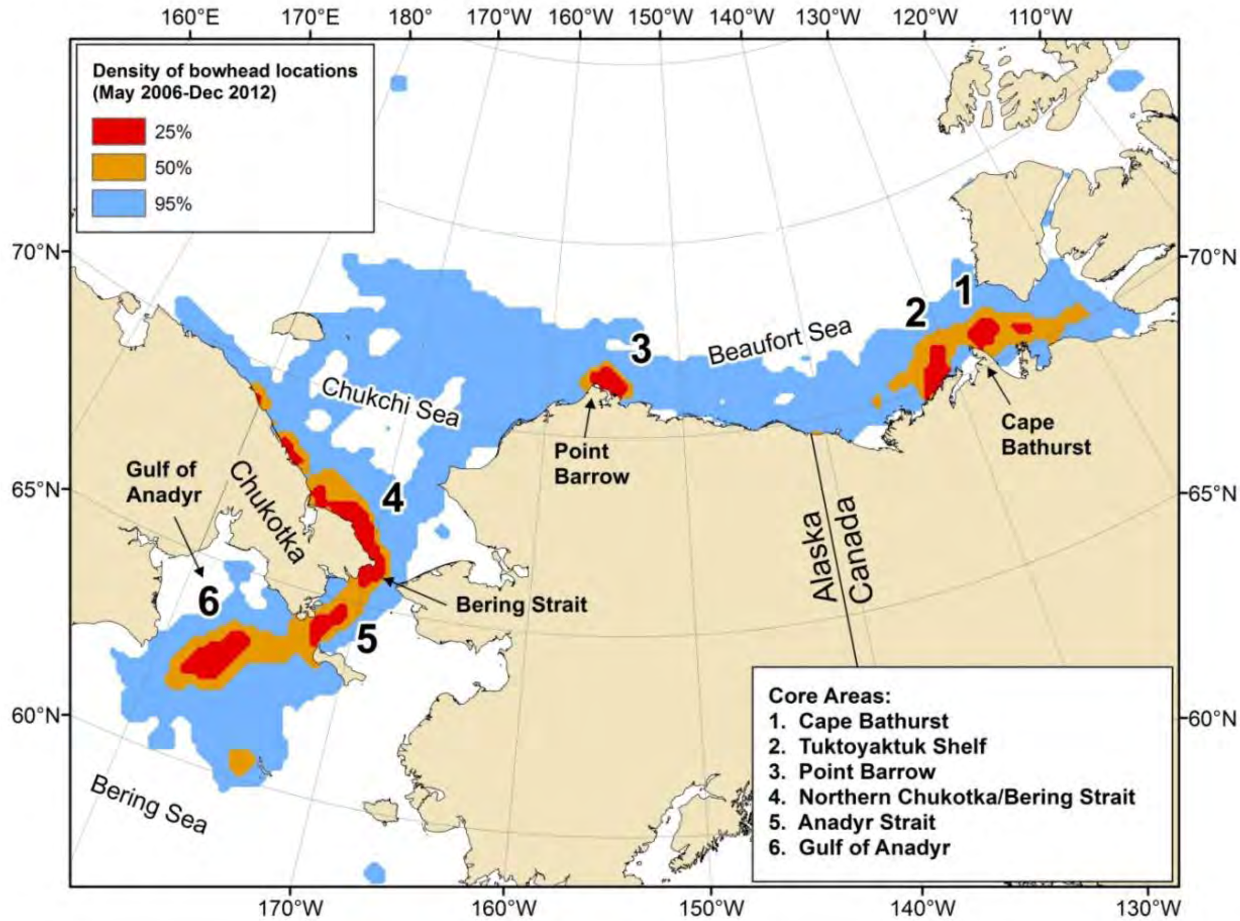

Figure 4. Utilization distribution for western Arctic bowhead whales with satellite tags, 2006-2011. Core areas, areas of high bowhead concentration, were defined as lying within the 25% density contours. Six primary core areas are identified. Figure from Citta et al. (2015).

During winter (late October–early January) whales congregated and moved slowly southward along the Chukotka coast, Russia (Area 4; Fig. 4), where zooplankton were likely concentrated along a coastal front between the Siberian coastal current flowing south-eastward and the Bering Sea waters flowing northward. Between late November and mid-April, bowheads were in the Bering Sea in Anadyr Strait (Area 5) and the Gulf of Anadyr (Area 6). Both areas were characterized by heavy but highly fractured sea ice. Whales in these areas spent much of the time near the bottom where overwintering copepods and euphausiids are expected to aggregate (Citta et al. 2012). We analysed 889 dive intervals (6-hr) and in all but five intervals (99.4%) tagged whales dove to the bottom at least once (Fig. 5). Water depths in the area ranged from 25 to 300 m (Quakenbush et al. 2010b; 2012). Such frequent use of the bottom supports feeding on an overwintering layer of copepods or euphausiids in winter. Bowhead use of these wintering areas ends in April with the timing of zooplankton ascent, well before the sea ice has withdrawn (Citta et al. 2015).

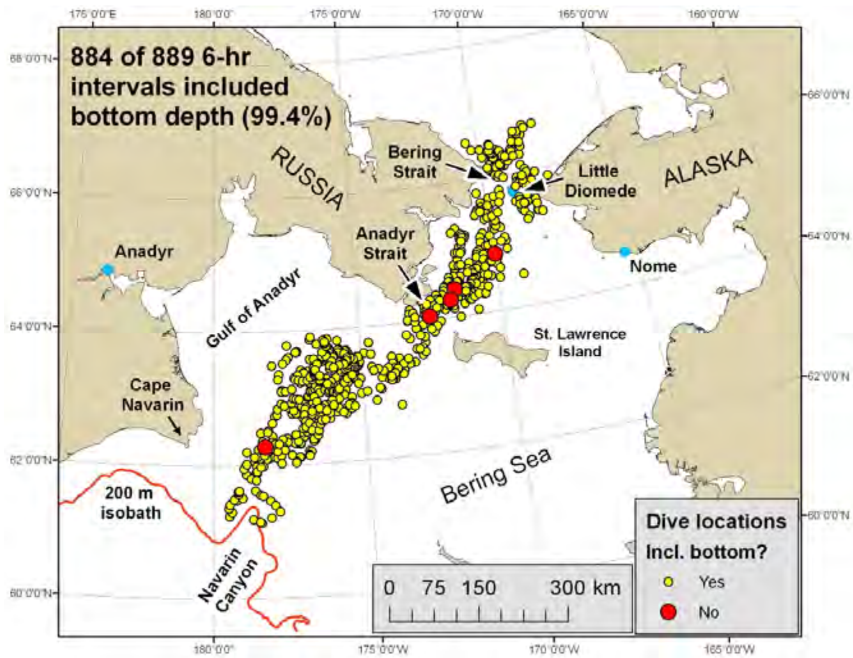

Figure 5. Tagged bowhead whale locations in the Bering Sea between January and April 2009 for which there are dive data. Red circles represent the only locations where a bowhead whale did not dive to the bottom during a 6-hr period. Nearly all dive intervals (99.4%) included the bottom. Figure from Quakenbush et al. (2012).

Also in winter, tagged whales used offshore areas of heavier, yet fractured, ice despite the availability of areas with open water near shore. Within a random sample of bowhead locations, only 1 of 102 locations (i.e., ~1%) fell within an open water area (polynya) during the winter of 2009/08 (Citta et al. 2012). Only 3 of 53 locations (~6%) fell within polynyas during the winter of 2009/10. Figure 6 shows the locations of seven tagged bowhead whales relative to ice and open water areas on 6 March 2009.

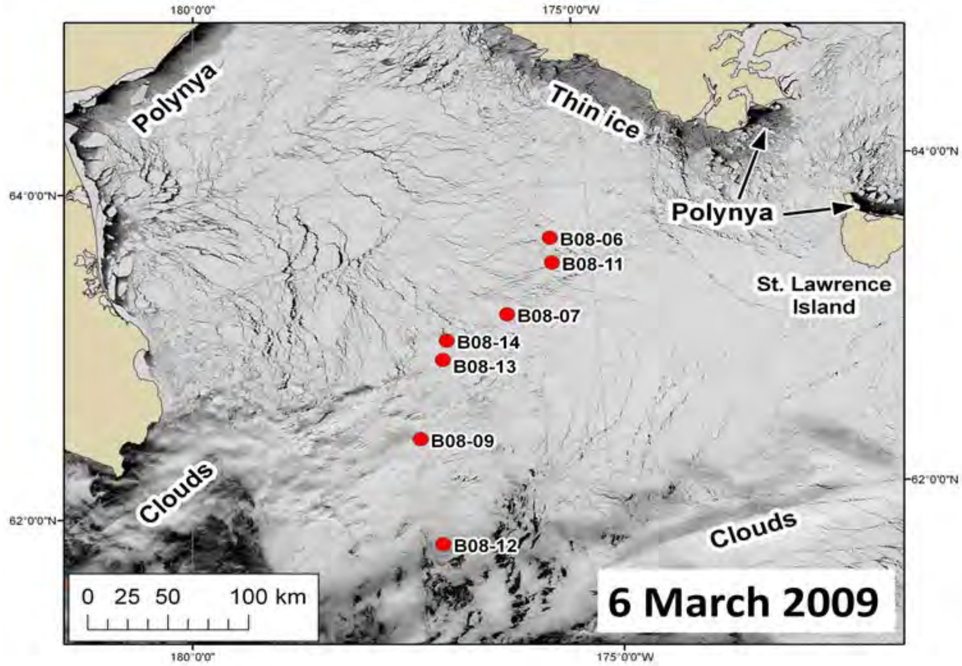

Figure 6. Locations of satellite-tagged bowhead whales (red circles) in March 2009 relative to open water areas (polynyas). Figure from Quakenbush et al. (2012).

The amount of sea ice present in this area in the winter of 2016/17 was remarkably low and there was no sea ice cover over much of the Gulf of Anadyr (Area 6). There were no tagged whales in winter 2016/17 to see how they responded to open water over much of their wintering area. If bowhead behavior was similar to that of the winters of 2008/09 and 2009/10, however, we would expect them to avoid the open water and move north or east or west rather than winter in open water (Fig. 7).

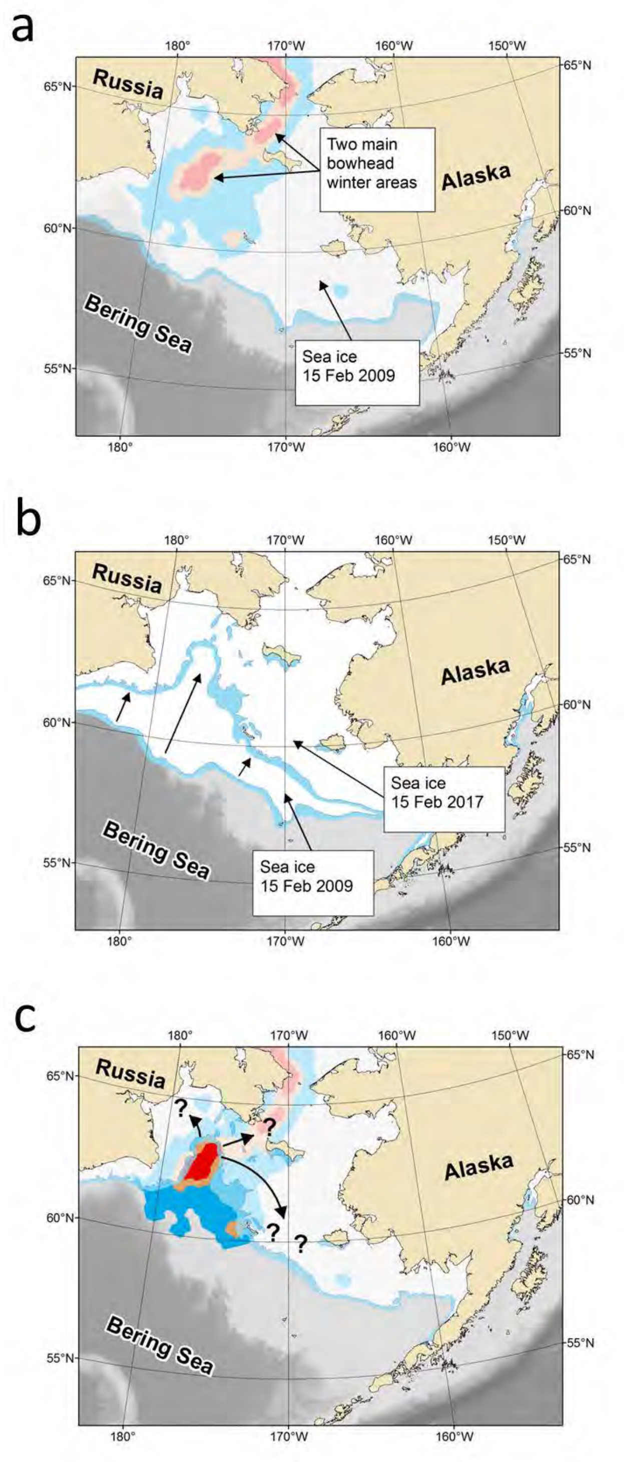

Figure 7. Sea ice extent in February 2009 (a) relative to two main bowhead whale winter areas. Change in ice extent between February 2009 and February 2017 (b) and sea ice extent in February 2017 relative to the two main bowhead whale winter areas. Question marks indicate that it is unknown where bowheads wintered because tagged bowheads have not wintered south of the ice edge or in open water during this study.

Movements and Variability of Movements. Movements among the core-use areas defined by Citta et al. (2015) appear to be timed with physical oceanographic conditions and the life history events of zooplankton (e.g., descent, ascent, and diapause) that affect the quality of an area for feeding rather than with ice retreat or formation. For example, the timing of when bowheads begin spring migration from the Bering Sea to Amundsen Gulf in the Canadian Beaufort Sea occurs before ice retreat such that bowheads are crossing the Beaufort Sea in May when the sea ice is at its heaviest of the year.

Although core-use areas are defined by repeated bowhead use, the timing and duration of use is variable. There are likely multiple ways that a core-use area may cease to be a quality feeding area. For example, zooplankton may not be present to up well even if winds are favorable, east winds may not be strong enough or last long enough, and alternatively they may last too long.

We have documented bowheads traveling to locations where they linger (assumed feeding) (Citta et al. 2015, Harwood et al. 2017) and to locations where they loop back to where they came from (Quakenbush et al. 2010, Quakenbush and Citta 2018). This return trip behavior may indicate low quality feeding at the time of the visit and a relatively low energetic cost of traveling to another location. Waiting for a location to develop into a good feeding area may include the chance that it will not develop, which may outweigh the energetic cost of traveling back to the previous feeding area or to a new potential feeding area.

The spring migration route appears to be fairly stable with bowheads leaving the Bering Sea and traveling along the Alaska coast past Point Barrow before turning east and crossing the Beaufort Sea (Fig. 11 in Quakenbush et al. 2012). Although there is often an east-west lead parallel to the coast, bowheads migrate north of it through heavy ice. The ice, however, is broken by the clockwise movement of the Beaufort Gyre (Fig. 8). This may be because the Amundsen Gulf feeding area is the only quality feeding area at that time of year and the quality may be highest early in the spring. As soon as the zooplankton concentration decreases in the Bering Sea there appears to be little incentive to stay and migration to Cape Bathurst begins.

The fall migration route is fairly stable westward in the Beaufort Sea but becomes more variable in the Chukchi Sea. Until 2017, bowheads traveling west generally stayed on or near the Beaufort shelf. One whale tagged in 2017 near Tuktoyaktuk, Canada, however traveled far offshore before heading west where it migrated over deep basin water (Quakenbush and Citta 2018).

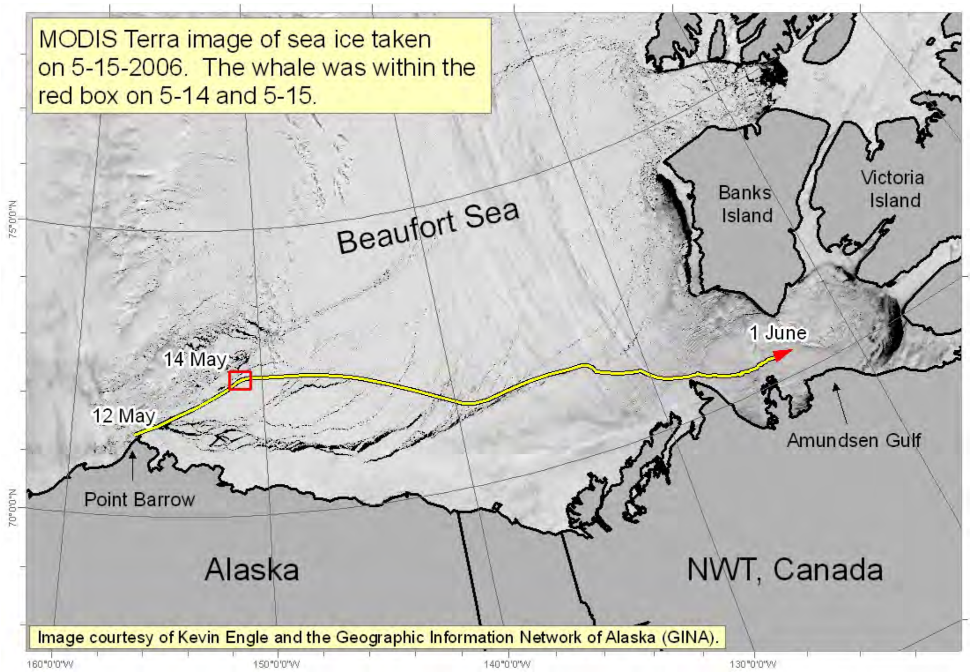

Figure 8. Spring migration route of B06-01showing the pattern of fracture of the sea ice caused by the Beaufort gyre, the east-west lead not used by bowheads, and the heavy ice in the Beaufort Sea during spring migration.

Once past Point Barrow, however, there is more variation in the route across the Chukchi Sea to the northern coast of Chukotka, Russia. Routes whales use when crossing the Chukchi Sea vary by year; in some years, whales migrate directly to the northern coast of Chukotka while in other years, whales may pause migration and linger, presumably to feed, in the central Chukchi Sea. To investigate how whale movements may be related to oceanographic variables we examined bowhead whale habitat selection within the Chukchi Sea in autumn (September–November) at two spatial scales (Citta et al. 2018). First, at the landscape scale (i.e. the Chukchi Sea), we compared oceanographic variables (e.g., temperature, salinity, and current velocity) at locations within used and randomly available tracks (i.e., paths of travel) to determine how oceanographic features are associated with where whales cross the Chukchi Sea in autumn. Second, at a local scale, we examine how directed travel or lingering within a whale's track is associated with oceanographic variables (e.g., temperature, salinity, and current velocity). Whale location data for 24 bowhead whales were paired with oceanographic data from a pan-arctic coupled ice-ocean model, the Regional Arctic System Model (RASM; Maslowski et al., 2012), for 2006–2009 and 2012. From 2006 to 2010 and in 2012, satellite tags provided enough location data to estimate locations and behaviors for 39 whales: 1 in 2006, 1 in 2007, 11 in 2008, 11 in 2009, 11 in 2010, and 4 in 2012.

We found two main movement patterns; bowhead whales spent relatively little time lingering within the central Chukchi Sea in 2008 and 2010 compared to 2009 and 2012 (Fig. 9). Neither the whale tagged in 2006 nor the one tagged in 2007 lingered in the central Chukchi, before reaching the Russian coast. These patterns could largely be explained by differences in how water masses were distributed.

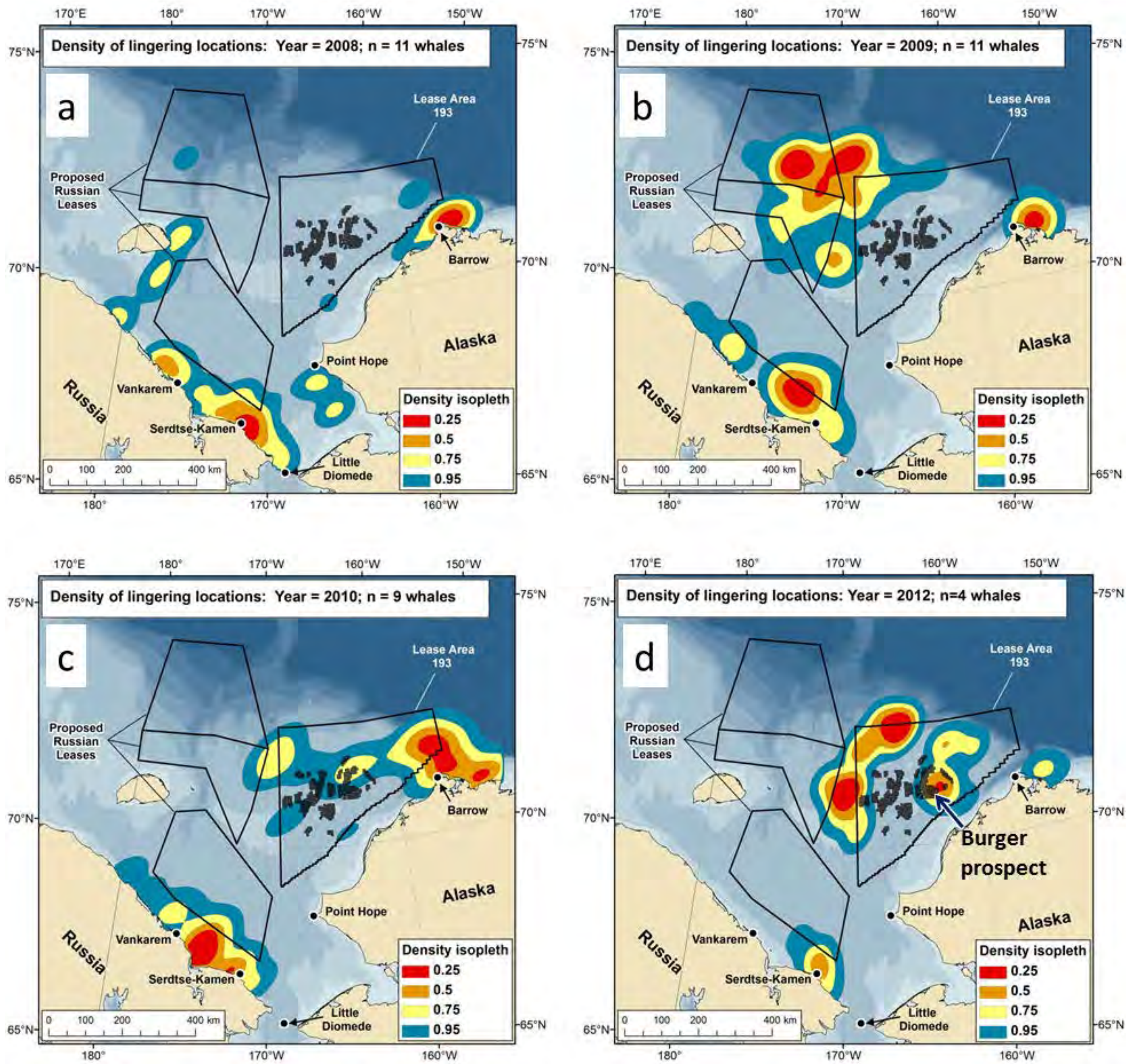

Figure 9. Kernel densities of bowhead whale locations classified as associated with lingering (presumed feeding) locations in the Chukchi Sea September–November in 2008, 2009, 2010, and 2012. Figure from Citta et al. (2018).

At the landscape scale, we found that whales generally followed water of Pacific origin characterized by temperatures < 0 ºC and salinities between 31.5–34.25 (Figs. 10 and 11). This water originates on the Bering Sea shelf and in the Gulf of Anadyr, and is known to have high densities of zooplankton (Eisner et al., 2013). In effect, bowhead whales are following the water masses that are more likely to have food. Bowhead whales avoided Alaskan Coastal Water and Siberian Shelf Water, the latter of which defines the western limit of their range. Both of these water masses are relatively fresh and they are both known to have lower densities of zooplankton (e.g., Eisner et al., 2013; Ershova et al., 2015). At the local scale, within whale tracks, whales were more likely to interrupt directed movements and linger in areas characterized by stronger gradients in bottom salinity (Fig. 12). This is likely because such gradients help aggregate zooplankton prey.

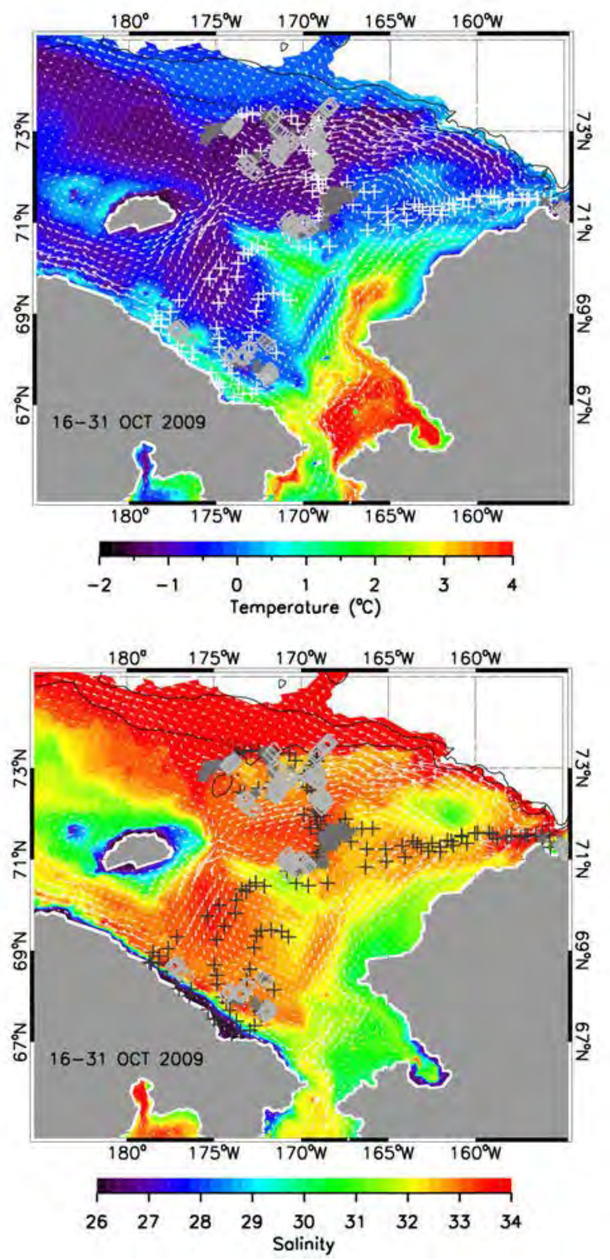

Figure 10. Example plot of temperature and salinity, averaged 16–31 October 2009. White arrows denote current vectors. Estimated bowhead whale locations and their behavior classifications overlie temperature and salinity layers. Crosses denote locations classified as "traveling", light gray open diamonds are classified as "lingering", and dark gray "x" denotes locations of unknown behavioral state. Figure from Citta et al. (2018).

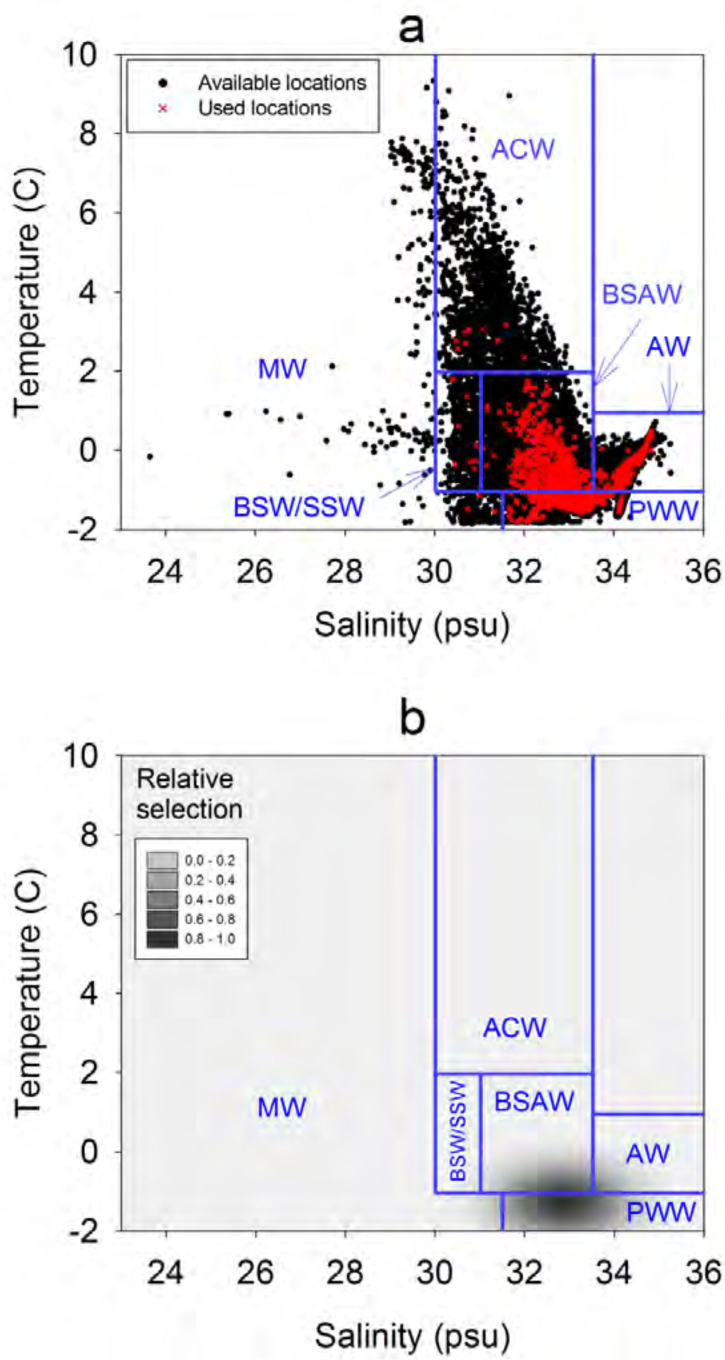

Figure 11. The distribution of all bowhead whale locations in temperature-salinity space (a) and the fit models of bowhead whale habitat selection based upon temperature and salinity (b). Tagged whales were most likely to occur in water -1.2 C and 32.75 psu; selection for other temperatures and salinities are scaled relative to this maximum. Blue boxes denote the approximate temperature-salinity signatures of different water masses, including melt water (MW), Alaskan Coastal Water (ACW), Bering Summer Water (BSW), Siberian Shelf Water (SSW), Bering Shelf/Anadyr Water (BSAW), Atlantic Water (AW), and Pacific Winter Water (PWW). Water mass boundaries are taken from Esiner et al. (2013), Gong et al. (2015), and Itoh et al. (2015). Figure from Citta et al. (2018).

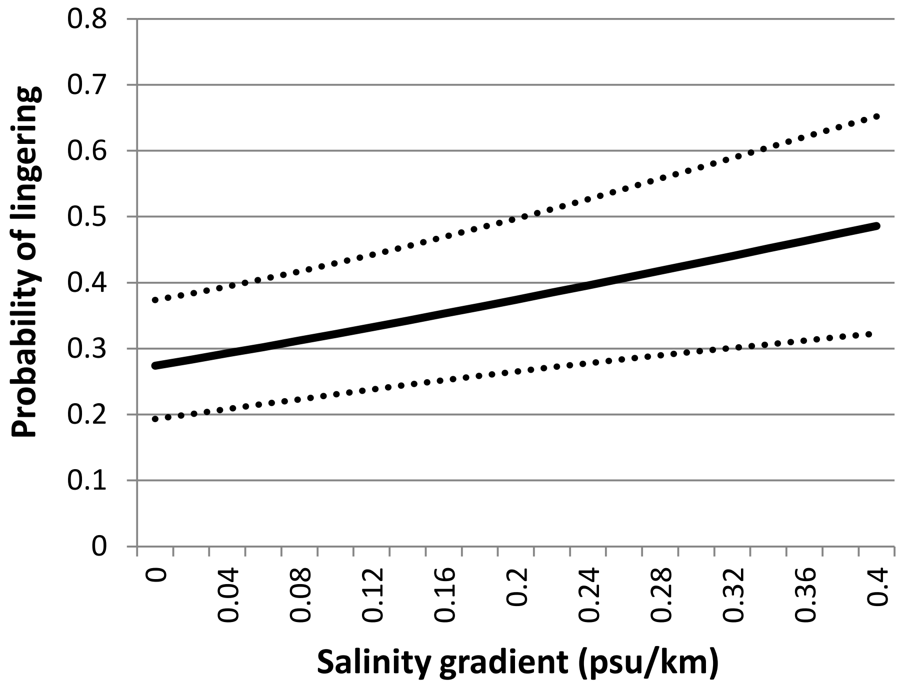

Figure 12. The probability of lingering (i.e., feeding) as a function of the maximum salinity gradient within 20 km. Dotted lines are 95% confidence limits. Figure from Citta et al. (2018).

Hence, we were able to largely explain the variation in how bowhead whales migrated across the Chukchi Sea, why bowheads do not typically migrate west of Wrangel Island (i.e., this is where relatively fresh Siberian Shelf Water occurs, which has a low density of zooplankton prey), and factors that help explain where whales pause to linger, such as salinity gradients that help aggregate prey. These relationships can be used to help predict how bowhead movements may shift as patterns in warming, winds, and/or currents change.

Prior to 2012, whales typically crossed the Chukchi Sea quickly and then traveled slowly southward along the Chukotka coast, eventually into the Bering Sea. In contrast to this, most whales in 2012 lingered within the Chukchi Sea Oil and Gas Lease Sale Area (Fig. 9d), co-occurring with drilling operations by Shell at the Burger Prospect. Whales remained in the central Chukchi Sea until sea ice formed along the northwestern coast of Chukotka. Whales then traveled to the coast of Chukotka near Bering Strait and entered the Bering Sea in early December. In 2009, whales also lingered in the north central Chukchi (Fig. 9b). During fall of 2017, one tagged whale (B17-02) entered the Chukchi Sea on 6 October from the north (through the Arctic Basin) and did not cross the Chukchi Sea shelf at all, but traveled to and along the Chukotka coast between Cape Schmidt and Vankarem from 20 October until 15 December when it left shore and by mid-January had joined the other whales tagged in 2017 lingering in the central Chukchi Sea between Vankarem, Russia, and Point Hope, Alaska. These other whales did not of migrate to the Russian coast but remained in the central Chukchi Sea until the end of January 2018 when they passed through Bering Strait into the Bering Sea.

Although we have demonstrated that bowheads prefer colder, saltier water masses (Fig. 11a and 11b) that are more likely to contain concentrations of zooplankton (Citta et al. 2018), why those water masses occasionally provide feeding opportunities in the Central Chukchi Sea is not known, but may be related to when northeast winds disrupt the Alaska Coastal current. Zooplankton are known to be advected onto the shelf near Point Barrow during east winds and get trapped when east winds slacken (i.e., “the krill trap”; Ashjian et al. 2010; Okkonen et al. 2011). However, when east winds persist, the “trap” may not develop and zooplankton may be advected west and available to bowheads in the north central Chukchi (Citta et al. 2018).

We have explored the physical oceanographic characteristics of core-use areas and found remarkable associations with conditions that concentrate weak swimming prey and the presence of bowhead whales (Citta et al. 2015, Citta et al. 2018). Alternatively, we have found that when those conditions break down, bowhead whales leave for another core-use area, and occasionally they loop back.

We have also explored the relationship of bowhead whales and sea ice. Ice cover has decreased more in the core-use areas, as defined by Citta et al. (2015), in the northern extent of bowhead range than in core-use areas in the southern extent. The number of open water days within the core-use areas near Point Barrow and along the northern Chukotka Coast during peak use has increased by 13 and 10 days/decade, respectively. The most dramatic reductions in sea-ice cover have taken place in the Alaskan Beaufort Sea where the number of open water days on the shelf and slope has increased by 20 and 25 days/decade, respectively (Druckenmiller et al. 2017). Using aerial survey data, we found that in the fall bowheads migrate closer to shore when there is less sea ice and farther from shore when there is more sea ice. We speculate that this might be because there are increased feeding opportunities closer to shore as a result of greater upwelling along the shelf break when the ice cover is farther from shore. Furthermore, the aerial survey data also revealed that high use areas within the Alaskan Beaufort Sea have shifted westward, toward Point Barrow, during fall in the period 1997–2014 compared to 1982–1996. As sea ice declines, we expect that northern core-use areas will be available to bowheads for longer periods, resulting in bowheads lingering in regions farther north through late fall, prior to entering the Bering Sea (see Discussion in Drukenmiller et al. 2017). The movement of bowhead whales away from the northern coast of Chukotka into the Bering Sea is correlated with ice formation and the breakdown of the strong coastal salinity front (Citta et al. 2015). Freeze-up restricts the input of fresh water entering the Siberian Coastal Current, weakening this front (see Fig. 8 in Citta et al., 2015) and possibly reducing the density of zooplankton. We would expect that a later freeze-up (as shown in Fig. 12) would lead to whales feeding along the northern Chukotka Coast for a longer period in fall. Salinity fronts created by Alaska Coastal water (Citta et al. 2018) may create similar feeding situations when Alaska Coastal Water plumes into the central Chukchi. We anticipate that bowheads will spend increasingly more time within summer and fall feeding areas, delaying their migration to the Bering Sea. Reduced ice coverage and thickness in the southern Chukchi Sea may make wintering there more common in the future. Indeed, the whales we tagged in 2017 delayed their entry into the Bering Sea until mid- to late-January 2018 and then returned north, well into the Chukchi Sea, in mid-February, when previous winter core-use areas that were ice-covered became ice free, possibly due to strong south winds.

Potential Disturbance. Commercial activities such as oil and gas exploration and development, fishing, and shipping have the potential to disrupt or displace bowhead movements, migrations, and feeding.

Oil and Gas: The areas of interest for oil and gas activities coincide in time and space with the major bowhead summer feeding area near the Tuktoyaktuk Peninsula in Canada (Fig. 13) and along the fall migration corridor in the Alaskan Beaufort Sea and in the Chukchi Sea (U.S. and Russia). For example, one tagged whale went through four active industrial areas in 2006, seismic operations were occurring in two of the areas when the whale passed (Fig. 14). If multiple seismic operations are planned in summer and fall within BCB bowhead range, timing should be coordinated to minimize interactions in time and space by multiple oil companies in multiple countries.

The one detailed occurrence of a tagged whale and a seismic operation suggested that when bowheads are feeding, the activities of a seismic operation may not totally displace whales from that feeding location. The closest distance of this whale to the ship conducting a 2-D seismic survey from 31 August to 4 October was 9.2 km. This whale remained in the active seismic area for 17 days. The whale left the area on 3 October to begin the westward migration, one day before the seismic operation was completed. This whale did not migrate early and such behavior suggests that feeding in this core-use area (Area 2 in Citta et al. 2015) is important and that feeding whales may be more tolerant of anthropogenic activities than migrating ones. This apparent tolerance of seismic activity also suggests that "ramping up" a seismic array so that the noise level increases slowly as airguns are turned on incrementally instead of all at once so that animals can leave the area before the noise reaches the maximum may not be effective for bowhead whales.

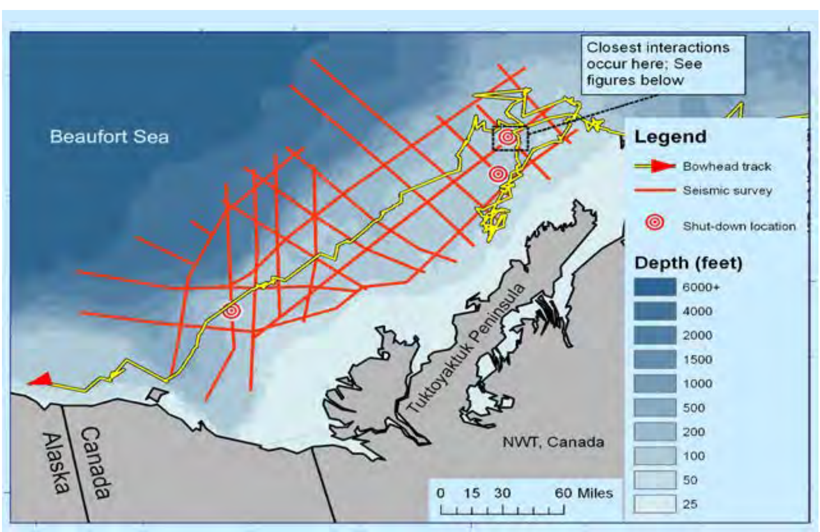

Figure 13. Tracks of a tagged bowhead whale (yellow line) within a marine seismic operation in the Canadian Beaufort Sea in 2006. The seismic operation occurred from 31 August to 4 October and the tagged whale remained in the seismic area from 16 September until 3 October when it began the westward migration. Note however the seismic area was identified as a core-use area (Area 2) by Citta et al. (2015) and likely important for feeding.

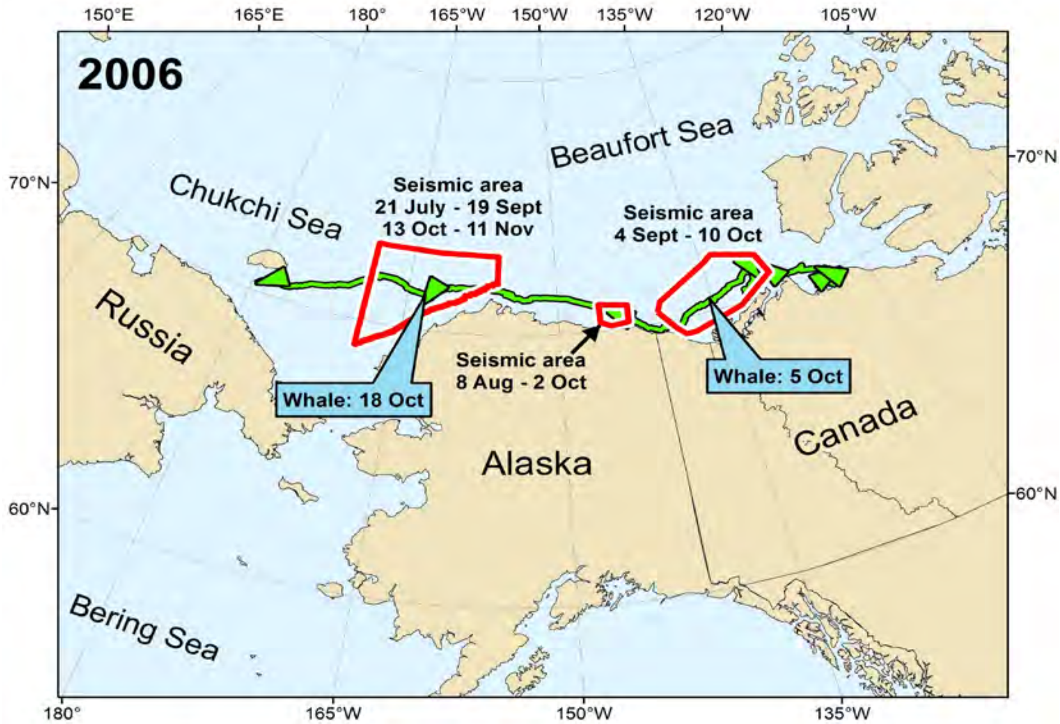

Figure 14. Track of a tagged bowhead whale and active industrial areas in 2006.

Commercial Fishing: Entanglement in fishing gear is a threat to bowhead whales. Harvested bowheads have a high incidence of scaring from lines thought to be mostly from pot gear used for cod and crab fishing in the Bering Sea (George et al. 2017). Bowhead whaling captains and the AEWC were concerned about the number of bowheads with scars from having been entangled and the number of whales towing gear. They requested an analysis of the overlap of tagged bowheads and the winter crab fisheries to better understand the spatial and temporal overlap and potential risk from entanglement. We analysed winter data from 21 tagged whales for the winters of 2008/09 and 2009/10 and found that in U.S. waters bowheads remained in areas with >90% ice cover, which is too heavy for crab boats to work in (Citta et al. 2014). Although pots are not dropped close to the ice edge, the ice can move quickly and overrun the active fishing gear, resulting in lost gear, which is the most likely cause of entanglement. During spring whaling near Utqiaġvik, Alaska, in 2017 two harvested bowheads were towing pot fishing gear (J.C. George, pers. comm.). Because there was so little ice in the Bering Sea in the winter of 2016/17 (Fig. 7) the whalers were concerned that bowheads were somehow becoming more vulnerable to entanglement in pot fishery gear. Another analysis showed that the pot fisheries in the U.S. had not moved north, however there were no tagged whales to provide information about bowhead distribution and use of the Bering Sea in that year. There are known to be Russian pot fisheries in the western Bering Sea as well, but no information could be found about the location and timing of their activities.

Commercial Shipping: Commercial shipping and ship-based tourism in the Arctic has increased as sea ice has decreased. Both shipping routes, the Northern Sea Route along the northern Russian coast, and the Northwest Passage through the Canadian Archipelago, go through Bering Strait. The entire population of BCB bowhead whales (>17,000 individuals) passes through Bering Strait each spring and fall between wintering and summering areas. As such, Bering Strait is an area of concern for interactions with ship traffic (Reeves et al. 2012). Ships traveling on the west side of the Diomedes and along the Chukotka coast between October and December could encounter a high proportion of the population (Figs. 15 and 16). Ship strikes in the Atlantic are the greatest source of mortality for right whales (*Eubalaena glacialis;* Moore et al. 2004). It is thought that bowhead whales may be as vulnerable to ship strikes as Atlantic right whales, due to their slow swimming speed and feeding behavior (Reeves et al. 2012); however, bowheads are known to be more sensitive and more difficult to approach during migration than when feeding(Richardson 1999).

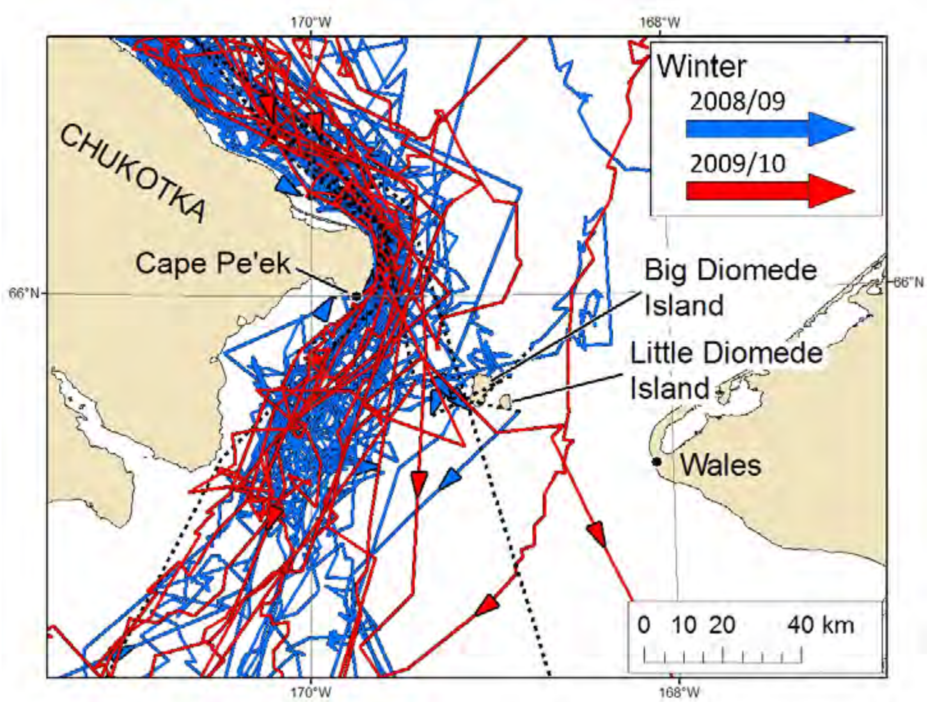

Figure 15. Tracks of tagged bowhead whales moving south through Bering Strait into the Bering Sea during the winters of 2008/09 (n=11) and 2009/10 (n=10). Dotted lines indicate connected locations that crossed landforms. Figure from Citta et al. (2012).

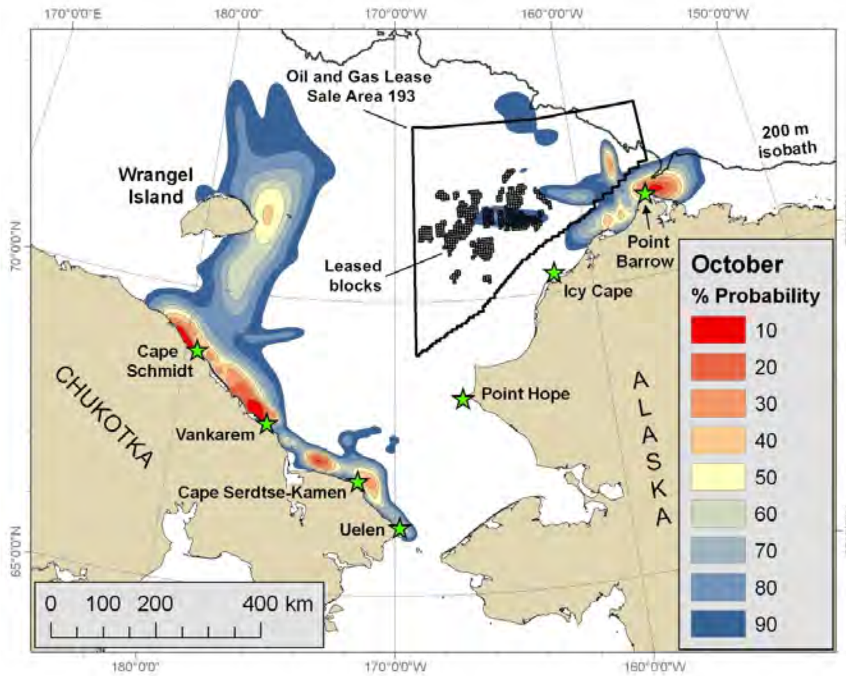

Figure 16. Kernel density contours showing the probability of use (%) by bowhead whales in October, 2006–2008. This is Figure 5 in Quakenbush et al. 2010a.

Evidence of Population Sub-structure. Satellite tagging studies are not ideal for studying stock structure if the location or movement behavior of separate stocks is unknown. For example, if two stocks existed and we tagged whales from one location, frequented by one stock, we may erroneously conclude that only one stock exists. With that said, satellite telemetry could identify separate stocks if individuals from each stock are tagged and then used winter, summer, or foraging areas unique to each stock. To-date, we have found no evidence from movements that sub-stock structure exists within the BCB stock. Whales tagged from St. Lawrence Island, Utqiaġvik, and a number of sites near the Mackenzie River Delta in Canada show similar movements.

Melnikov and Zeh (2007) documented whales migrating past Cape Pe'ek, on the Russian side of Bering Strait. Based upon swim speeds and the late date of observations, it was unlikely that these whales were migrating past Point Barrow—if they did it would have been mid-to-late June. As such, whales that summer along the Russian coast in the Chukchi Sea are the most likely candidate for a separate stock within the BCB population. However, movement data do not support the idea that there might be spatially distinct populations in summer. To-date, every tagged whale but one has migrated to the Canadian Beaufort in spring. The only whale that did not migrate to the Canadian Beaufort was B09-09, which was tagged near Point Barrow in the fall of 2009. The following year, this whale summered along the Russian coast of the Chukchi Sea (see Citta et al. 2012). We think it unlikely that this whale returned to Point Barrow that fall.

It is unlikely that whales summering in the Chukchi Sea are spatially separated from whales that summer in the Canadian Beaufort. The whale that summered in the Chukchi (B09-09) was tagged near Point Barrow and was likely migrating from the Canadian Beaufort (although this is unknown). Furthermore, we have observed that many other tagged whales leave the Canadian Beaufort Sea in mid-summer and migrate to this same area along the Russian coast in the Chukchi Sea. Such movements from the Canadian Beaufort to the Russian coast occurred in the summer of 2010 and 2012.

In addition, we found no evidence of spatial segregation on the wintering grounds (also the breeding season) in the Bering Sea. Although two main wintering areas have been identified (Area 5 and Area 6; Fig. 4; Citta et al. 2015), most whales use both areas in the same winter. Of the 28 whales that used Area 5 (Anadyr Strait), 19 (70%) also used Area 6 (Gulf of Anadyr). Furthermore, Areas 5 and 6 are not truly distinct because the entire corridor from Bering Strait, through Anadyr Strait, to the shelf break received high use and is within the 50% core use area. A difference in use between the two areas is more likely determined by sea ice extent. Bowhead whales do not typically migrate south of the sea ice boundary and the southernmost parts of their range are often ice-free.

Hence, the movement data collected to-date have not identified separate feeding or wintering areas that might be indicative of separate stocks.

Summary. In general, movements of tagged bowhead whales described here are consistent with published literature regarding migratory behavior (Braham et al. 1979, Moore et al. 1995, Mate et al. 2000, Moore and Reeves, 1993). However, our study provided new information including:

1) specific wintering areas, affinity for sea ice, and diving to the bottom in the Bering Sea;
2) a whale that did not pass Barrow on the spring migration, summered in the Chukchi Sea, and would not have been counted during spring ice-based surveys;
3) extensive summer movements include travel far to the north and northeast overlapping with bowheads from the Baffin Bay-Davis Strait stock, summer travel between Canada and Barrow, and between Canada and the Chukchi Sea, in addition to the spring and fall migrations;
4) fall movements coincided in space and time with industrial activities (i.e., oil and gas, potentially shipping);
5) six core-use areas were identified as probable feeding areas; these areas include: Amundsen Gulf, Tuktoyaktuk Shelf, Point Barrow, Chukotka coast, and two areas in the Bering Sea;
6) annual variability in migration routes and timing especially across the Chukchi Sea; and
7) recent changes in summer movements (i.e., greater use of mid and western Beaufort Sea) and speculated less use of previous core-use areas in the Bering Sea in winter that were largely ice-free in winter 2016/17 and 2017/18.

This telemetry study was not designed to address stock sub-structure, and more widely distributed tagging locations would be better for such an analysis. Nevertheless, none of the movements from tagged whales suggest a multi-stock condition exists within BCB bowhead whales. The one whale that did not pass Point Barrow in the spring and instead summered in the Chukchi Sea was tagged near Point Barrow in August the previous year. This behavior suggests that individuals may change their summer areas from year to year, possibly due to their reproductive condition. For the two BCB whales that traveled into the range of the Baffin Bay-

Davis Strait stock, both did so during the non-breeding season and both returned to their respective stock's range in fall prior to the normal fall migration.

ACKNOWLEDGMENTS
This project would not be possible without the hard work and intense interest of many people including the following cooperators: the North Slope Borough, the Alaska Eskimo Whaling Commission, the Barrow and Kaktovik Whaling Captains' Associations, Aklavik and Tuktoyaktuk Hunters and Trappers Committees, the Department of Fisheries and Oceans Canada, and the Greenland Institute of Natural Resources. Taggers included Harry Brower, Jr., Lewis Brower, Billy Adams, George Tagarook, James Pokiak, Charles Pokiak, and Gary Raddi, Jr. Robert Small assisted with tagging and logistics in Canada. Mikkel and Anders Villum Jensen built the tagging equipment and assisted with tagging. Stephen Okkonen provided valuable oceanographic information, insight and interpretation. GX Technology provided seismic data for 2006. Funding was provided by the U.S. Minerals Management Service (now the Bureau of Ocean Energy Management) with assistance from Charles Monnett, Jeffery Denton, and Carol Fairfield. Additional funding for tagging in Canada was provided by the Fisheries Joint Management Committee, Ecosystem Research Initiative and the Panel for Energy Research and Development. Research was conducted under the following permits in the U.S.: NMFS 782-1719 and 14610, 18890; ADF&G IACUC 06-16, 09-21, 2010-13R, 2012-20, 2013-20, 2014-03, 2015-25, and 2016-23.; and in Canada In Canada, research was conducted under Department of Fisheries and Oceans Scientific License Nos. S-07/08-4007-IN, S-08/09-4000-IN, S-09/10-4005-IN-A1, S-14/15-1027-NU, S-16-17-3035-YK Lea, and Animal Care Protocols FWI-ACC-2007-2008-013 and FWI-ACC-2008-031, FWI-ACC-2009-019, FWI-ACC-2014-048, AUP 2016-045.

REFERENCES
Braham, H., B. Krogman, S. Leatherwood, W. Marquette, D. Rugh, M Tillman, J. Johnson, and G. Carroll. 1979. Preliminary report of the 1978 spring bowhead whale research program results. Report of the International Whaling Commission 29:291–306.

Christman, C.L., J.J. Citta, L.T. Quakenbush, J.T. Clarke, B.K. Rone, R.A. Shea, M.C. Ferguson, and M.P. Heide-Jørgensen. 2013. Presence and behavior of bowhead whales (*Balaena mysticetus*) in the Alaskan Beaufort Sea in July 2011. Polar Biology, doi: 10.1007/s00300-013-4.

Citta, J.J., L.T. Quakenbush, S.R. Okkonen, M.L. Druckenmiller, W. Maslowski, J. Clement-Kinney, C.J. Ashjian, J.C. George, H. Brower, R.J. Small, L.A. Harwood, and M.P. Heide-Jørgensen. 2015. Ecological characteristics of core-use areas used by Bering-Chukchi-Beaufort (BCB) bowhead whales, 2006–2012. Progress in Oceanography 136:201–222, http://dx.doi.org/10.1016/j.pocean.2014.08.012

Citta, J.J., L.T. Quakenbush, J.C. George, R.J. Small, M.P. Heide-Jørgensen, H. Brower, B. Adams, and L. Brower. 2012. Winter movements of bowhead whales (*Balaena mysticetus*) in the Bering Sea. Arctic 65(1):13–34.

Citta, J.J., J.J. Burns, L.T. Quakenbush, V. Vanek, J.C. George, R.J. Small, M.P. Heide-Jorgensen, and H. Brower. 2014. Interactions of bowhead whales and winter pot fisheries in the Bering Sea. Marine Mammal Science 30:445-459. DOI: 10.1111/mms.12047

Citta, J.J., L.T. Quakenbush, S.R. Okkonen, M.L. Druckenmiller, W. Maslowski, J. Clement-Kinney, J.C. George, H. Brower, R.J. Small, C.J. Ashjian, L.A. Harwood and M.P. Heide-Jørgensen. 2015. Ecological characteristics of core areas used by western Arctic bowhead whales, 2006-2012. Progress in Oceanography 136:201–222, http://dx.doi.org/10.1016/j.pocean.2014.08.012

Citta, J.J., S.R. Okkonen, L.T. Quakenbush, W. Maslowski, R. Osinski, J.C. George, R.J. Small, H. Brower, M.P. Heide-Jørgensen, and L.A. Harwood. 2018. Oceanographic characteristics associated with autumn movements of bowhead whales in the Chukchi Sea. Deep-Sea Research II.

Druckenmiller, M.L., J.J. Citta, M.C. Ferguson, J.T. Clarke, J.C. George, and L. Quakenbush. 2017. Trends in sea-ice cover within bowhead whale habitats in the Pacific Arctic. Deep-Sea Research Part II, https://doi.org/10.1016/j.dsr2.2017.10.017

Duong, T. 2007. ks: Kernel density estimation and kernel discriminant analysis for multivariate data in R. Journal of Statistical Software 21(7):1–16.

Duong, T., and M.L. Hazelton. 2005. Cross-validation band-width matrices for multivariate kernel density estimation. Scandinavian Journal of Statistics 32(3):485–506.

Ershova, E.A., Hopcroft, R.R., Kosobokova, K.N., Matsuno, K., Nelson, R.J., Yamaguchi, A., Eisner, L.B., 2015. Long-term changes in summer zooplankton communities of the western Chukchi Sea, 1945–2012. Oceanography 28:100–115.

Esiner, L., Hillgruber, N., Martinson, E., Maselko, J., 2013. Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi seas. Polar Biology 36:87–113.

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

George, J.C., J. Zeh, R. Suydam, and C. Clark. 2004. Abundance and population trend (1978–2001) of western Arctic bowhead whales surveyed near Barrow, Alaska. Marine Mammal Science 20(4):755–773.

George, J.C., G. Sheffield, D.J. Reed, B. Tudor, R. Stimmelmayr, B.T. Person, T. Sformo, and R. Suydam. 2017. Frequency of injuries from line entanglements, killer whales, and ship strikes on Bering-Chukchi-Beaufort Seas bowhead whales. Arctic 70(1):37–46.

Givens, G.H., S.L. Edmondson, J.C. George, B. Tudor, R.A. DeLong, and R. Suydam.2015. Horvitz-Thompson whale abundance estimation adjusting for uncertain recapture, temporal availability variation, and intermittent effort. Envirometrics (wileyonlinelibrary.com; DOI: 10.1002/env.2379).

Harwood, L.A., L.T. Quakenbush, R.J. Small, J.C. George, J. Pokiak, C. Pokiak, M.P. Heide-Jørgensen, E.V. Lea, and H. Brower. 2017. Movements and inferred foraging by bowhead whales in the Canadian Beaufort Sea during August and September, 2006–12. Arctic 70(2):161–176.

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

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

Heide-Jørgensen, M.P., Laidre, K.L., L.T. Quakenbush, and J.J. Citta. 2011. The Northwest Passage opens for bowhead whales. Biology Letters doi: 10.1098/rsbl.2011.0731.

Maslowski W., J. Clement Kinney, M. Higgins, and A. Roberts. 2012. The future of arctic sea ice. Annual Review of Earth and Planetary Sciences. 40:625–654.

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

Melnikov, V., and J. Zeh. 2007. Chukotka Peninsula counts and estimates of the number of migrating bowhead whales. SC/58/BRG15.

Moore, M.J., A.R. Knowlton, S.D. Kraus, W.A. McLellan, and R.K. Bonde. 2004. Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities (1970–2002). Journal of Cetacean Research and Management 6(3):199–214.

Moore, S.E., and R.R Reeves. 1993. Distribution and movement. Pages 313–386 *in:* J.J. Burns, J.J. Montague and C.J. Cowles (eds.). The Bowhead Whale. Special Publication No. 2, Society for Marine Mammalogy.

Moore, S.E., J.C. George, K.O. Coyle, and T.J. Weingartner. 1995. Bowhead whales along the Chukotka coast in autumn. Arctic 48(2):155–160.

Quakenbush, L., and J. Citta. 2018. Satellite tracking of bowhead whales: habitat use, passive acoustic and environmental monitoring. Annual report to BOEM #M12PC00005. 88 pp.

Quakenbush, L.T., J.J. Citta, J.C. George, R.J. Small, and M.P. Heide-Jørgensen. 2010a. Fall and winter movements of bowhead whales (*Balaena mysticetus*) in the Chukchi Sea and within a potential petroleum development area. Arctic 63(3):289–307.

Quakenbush, L.T., R.J. Small, and J.J. Citta. 2010b. Satellite Tracking of western Arctic bowhead whales. Final Report. OCS Study BOEMRE 2010-033. 65 pp w/o appendices.

Quakenbush, L., J. Citta, J.C. George, M.P. Heide-Jørgensen, R. Small, H. Brower, L. Harwood, B. Adams, L. Brower, G. Tagarook, C. Pokiak, and J. Pokiak. 2012. Seasonal movements of the Bering-Chukchi-Beaufort stock of bowhead whales: 2006–2012 satellite telemetry results. International Whaling Commission Scientific Report SC/64/BRG1.

Quakenbush, L., J. Citta, and R. Small. 2016. Satellite tracking of bowhead whales: habitat use, passive acoustic and environmental monitoring. Annual report to BOEM #M12PC00005. 40 pp.

Reeves, R., C. Rosa, J.C. George, G. Sheffield, and M. Moore. 2012. Implications of Arctic industrial growth and strategies to mitigate future vessel and fishing gear impacts on bowhead whales. Marine Policy 36:454–462.

Richardson, W.J. (ed.) 1999. Marine mammal and acoustical monitoring of Western Geophysical's open-water seismic program in the Alaskan Beaufort Sea, 1998. LGL Rep. TA2230-3. Report from LGL Ltd., King City, Ont., and Greenridge Sciences Inc., Santa Barbara, CA, for Western Geophysical, Huston, TX, and National Marine Fisheries Service, Anchorage, AK., and Silver Spring, MD. 390 pp.

Wand, M.P., and M.C. Jones. 1995. Kernel smoothing. London: Chapman & Hall. 212 pp.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Zeh, J.E., C.W. Clark, J.C. George, D. Withrow, G.M. Carroll, and W.R. Koski. 1993. Current population size and dynamics. Pages 409–489 *in:* J.J. Burns, J.J. Montague, and C.J. Cowles (eds.). The Bowhead Whale. Special Publication No. 2, Society for Marine Mammalogy.