



Satellite telemetry reveals population specific winter ranges of beluga whales in the Bering Sea

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ABSTRACT

At least five populations (stocks) of beluga whales (*Delphinapterus leucas*) are thought to winter in the Bering Sea, including the Bristol Bay, Eastern Bering Sea (Norton Sound), Anadyr, Eastern Chukchi Sea, and Eastern Beaufort Sea (Mackenzie) populations. Belugas from each population have been tagged with satellite-linked transmitters, allowing us to describe their winter (January–March) distribution. The objectives of this paper were to determine: (1) If each population winters in the Bering Sea, and if so, where? (2) Do populations return to the same area each year (*i.e.*, are wintering areas traditional)? (3) To what extent do the winter ranges of different populations overlap? Tagged belugas from all five populations either remained in, or moved into, the Bering Sea and spent the winter there. Each population wintered in a different part of the Bering Sea and populations with multiple years of data (four of five) returned to the same regions in multiple years. When data were available from two populations that overlapped in the same year, they did not occupy the shared area at the same time. Although our sample sizes were small, the evidence suggests belugas from different populations have traditional winter ranges that are mostly exclusive to each population.

Key words: beluga whales, *Delphinapterus leucas*, Bristol Bay, Bering Sea, Gulf of Anadyr, Chukchi Sea, Beaufort Sea, satellite-linked transmitters, winter distribution.

Beluga whales (*Delphinapterus leucas*) are widely distributed in arctic and subarctic waters with at least 19 populations (stocks) identified worldwide (IWC 2000, Laidre *et al.* 2015). At least five populations have been identified within the Bering, Chukchi, Beaufort, and East Siberian Seas. Our understanding of the distribution of beluga populations in the western Arctic was initially based upon traditional subsistence harvest areas used by the Alaska Natives during April–October (Frost and Lowry 1990), aerial surveys conducted in the Beaufort and Chukchi Seas during spring, summer, and fall (*e.g.*, Braham *et al.* 1984), and sightings of belugas in the Russian Arctic (Kleinenberg *et al.* 1964). Results showed that belugas are regularly found during summer in Bristol Bay, the eastern Bering Sea (EB; Norton Sound and the Yukon River delta), and the eastern Chukchi Sea (ECS; Kasegaluk Lagoon) in Alaska (Seaman and Burns 1981, Frost and Lowry 1990); the Gulf of Anadyr in eastern Russia (National Marine Mammal Lab [NMML], unpublished data); and the eastern Beaufort Sea (EBS;² Mackenzie River delta) in western Canada (Fraker *et al.* 1979, Harwood *et al.* 1996). These five groups are recognized as separate populations (*e.g.*, Allen and Angliss 2014; Fig. 1) based upon their summer distribution and genetic differentiation (O’Corry-Crowe *et al.* 1997, 2002, 2010).

Our understanding of how beluga populations are distributed has been refined by the use of satellite data recorders (SDRs), which have been attached to individuals in all five populations. Tagging studies show that ECS belugas tagged at Kasegaluk Lagoon ranged throughout the eastern Chukchi and Beaufort Seas in summer (Suydam *et al.* 2001, Suydam 2009, Hauser *et al.* 2014), while EBS belugas tagged in the Mackenzie Delta summer farther east in the Beaufort Sea, near the Mackenzie Delta and in the western Canadian Archipelago (Richard *et al.* 2001, Hauser *et al.* 2014). In contrast, belugas tagged in Bristol Bay remain in Bristol Bay year-round (Citta *et al.* 2016). Results for the Anadyr and EBS populations have yet to be fully analyzed.

Much less is known about the winter ranges of western Arctic beluga populations. The winter range of the Bristol Bay population was described by Citta *et al.* (2016) and that of the eastern Beaufort Sea population was described by Luque and Ferguson (2010), however, it is generally assumed that most western Arctic belugas winter in the Bering Sea, with some wintering in the southern Chukchi Sea (*e.g.*, Braham *et al.* 1984, Frost and Lowry 1990). Here we bring together the location data for all five populations and address the following questions: (1) Do belugas from each population winter in the Bering Sea, and if so, where? (2) Do beluga populations have traditional wintering areas (*i.e.*, are the same areas used year-after-year)? (3) Do the wintering ranges of different populations overlap, and if so, to what extent? To address these questions, we present all available location information from satellite-linked transmitters attached to western Arctic belugas during October–May, 2001–2013.

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²Belugas summering in the eastern Beaufort Sea are referred to as the Beaufort Sea population in the United States and as the Eastern Beaufort Sea population in Canada. To avoid confusion in the abbreviations between the Eastern Bering Sea and the Eastern Beaufort Sea populations, we use EB to denote the Eastern Bering Sea belugas and EBS to denote Eastern Beaufort Sea belugas.

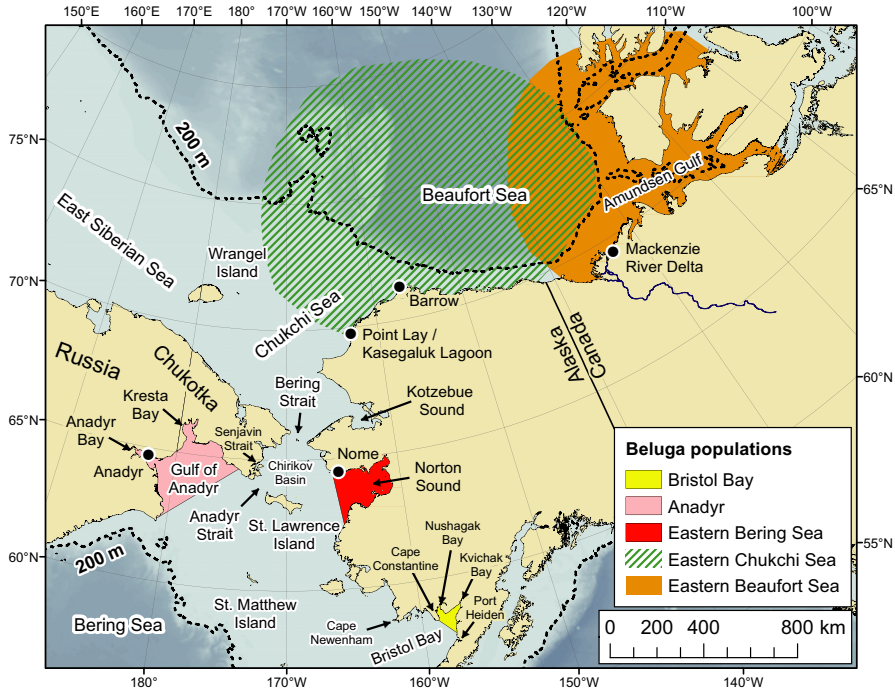


Figure 1. Approximate summer ranges for beluga populations thought to winter in the Bering Sea.

METHODS

Most of the belugas used in this study were captured using the methods described by Orr *et al.* (1998), by which belugas in shallow water are either encircled with large-mesh seine nets deployed from boats or caught with hoop nets that are slipped over the head and shoulders, either from boats or by people standing in shallow water. Belugas from the Bristol Bay (Citta *et al.* 2016), Anadyr (Hobbs *et al.* 2007), EBS (Richard *et al.* 2001) and ECS (Suydam *et al.* 2001, Suydam 2009) populations were captured in this fashion. Prior to capture, ECS belugas were herded into Kasegaluk Lagoon near Point Lay during the annual community hunt. Native subsistence hunters use boats to direct belugas from the Chukchi Sea through a pass between barrier islands and into the shallow water of Kasegaluk Lagoon, where they are harvested. Belugas not harvested were available for capture. Belugas from EB population were captured in stationary nets used for the Alaska Native subsistence harvest near Nome, Alaska. Information regarding the tagged belugas analyzed in this study and the tag duty cycle is provided in Appendix S1. Although many more belugas have been tagged, we limit our description to those transmitters that lasted into October of the year in which they were tagged.

Satellite locations were collected *via* the Advanced Research and Global Observation Satellite (ARGOS) data collection and location system (Fancy *et al.* 1988, Rodgers 2001). When processing the location data, we first used a filter that removed locations resulting in velocities greater than a fixed threshold (McConnell *et al.*

1992). A threshold of 1.78 m/s was chosen after considering a variety of sources. Smith and Martin (1994) found belugas traveling at 1.4 m/s, Lydersen *et al.* (2001) documented 1.67 m/s as a maximum sustained velocity, and Richard *et al.* (2001) documented velocities of 1.17–1.78 m/s, which included the fastest observed velocity in any of the studies. After filtering the data, we removed locations that fell on land.

Because we are working with few tagged whales per population (Appendix S1), we relied on simple analyses. We summarized the timing of movements into and out of the Bering Sea based upon the time-stamp of filtered locations. Home ranges were defined using the minimum convex polygon derived from all locations that passed the velocity and land filters. To provide a general description of ice conditions in the Bering Sea, we averaged sea ice concentration data by month during the study period (October 2001–May 2013) using Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data available at the National Snow and Ice Data Center (<https://nsidc.org/>). In 2012, the year in which belugas from multiple stocks were tagged, we overlaid the location data with daily (2012) passive microwave sea ice data from the National Ice Center (NIC) (<http://www.natice.noaa.gov/index.html>) and examined the spatial and temporal overlap between whales from different populations.

RESULTS

Bristol Bay Population

In Bristol Bay, 29 SDRs provided location data between October and May (sample sizes provided in Fig. 2, 3, Appendix S1). Bristol Bay belugas moved out of the inner bays (Kvichak and Nushagak Bays) in winter, but never ranged west of Cape Newenham, and therefore remained within greater Bristol Bay (Fig. 2, 3). The earliest a Bristol Bay beluga ranged west of Cape Constantine was 23 November (in 2012); however, the average date Bristol Bay belugas first moved west of Cape Constantine was 22 December ($n = 15$ belugas) and belugas typically did not approach Cape Newenham until February (Fig. 3). Some Bristol Bay belugas also wintered along the southern shore of Bristol Bay. One beluga ranged as far west as Port Heiden during 28–29 January 2012 (Fig. 2). In May, the range of Bristol Bay belugas contracted back into Kvichak and Nushagak Bays (Fig. 3).

Anadyr Population

Belugas in the Anadyr population were captured and tagged in July and August, and five SDRs provided locations during October–May (Appendix S1). Two of the five transmitters provided location data into January of the following year, one into February, one into April, and one transmitted until the following July. In October, Anadyr belugas were largely limited to Anadyr Bay. In November and December, Anadyr belugas were located throughout the Gulf of Anadyr, in Anadyr and Kresta Bays, and along the continental shelf west of Cape Navarin (Fig. 2). Anadyr belugas were not located within Anadyr or Kresta Bays after early December; the latest a beluga was located in one of those bays was 6 December, when a single beluga was in Kresta Bay.

As winter progressed, the distribution of Anadyr belugas shifted southwest from the inner bays. At this time, the range of Anadyr belugas extended from the vicinity of Cape Navarin to Olytorsky Bay (Fig. 2, 3). Four of the five Anadyr belugas were

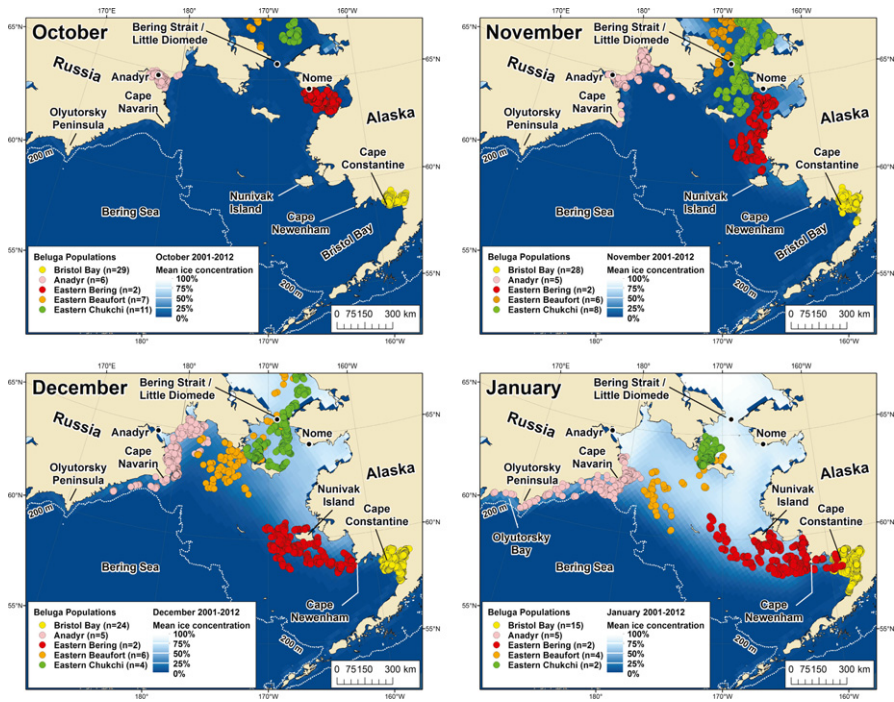


Figure 2. Beluga whale locations by population and month, October–January, all years pooled. Sea ice concentrations are Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data available at the National Snow and Ice Data Center (<https://nsidc.org/>). Concentration data were averaged by month during the study period (October 2001–January 2013).

located southwest of Cape Navarin. The earliest a beluga passed east of Cape Navarin was 26 December and the latest location east of the cape was 19 April. One beluga did not pass east of Cape Navarin before the tag stopped transmitting on 21 January 2002. Another beluga (AN08-02) traveled west of the Olyutorsky Peninsula, into Olyutorsky Bay, from 17 to 19 January 2008. Locations south and west of Cape Navarin were generally clustered along the shelf break (Fig. 2, 3).

Only one tag transmitted into May. This beluga (AN08-02) left Cape Navarin and headed north toward Anadyr Bay on 19 April and on 31 May was located at the mouth of Anadyr Bay (Fig. 3).

Eastern Bering Sea (EB) Population

Two EB belugas were tagged near Nome, Alaska, on 29 September and 14 October 2012 (Appendix S1). Prior to November, both belugas ranged throughout Norton Sound (Alaska Beluga Whale Committee, unpublished data). The first beluga left Norton Sound on 7 November and reached Nunivak Island by 1 December, and by 13 December it was located near Bristol Bay. The second beluga left Norton Sound on 14 November and was west of Nunivak Island by 2 December (Fig. 2). This beluga did not enter Bristol Bay. In April and May, the two belugas began to move northwards (Fig. 3). Movement towards Norton Sound was not direct; both

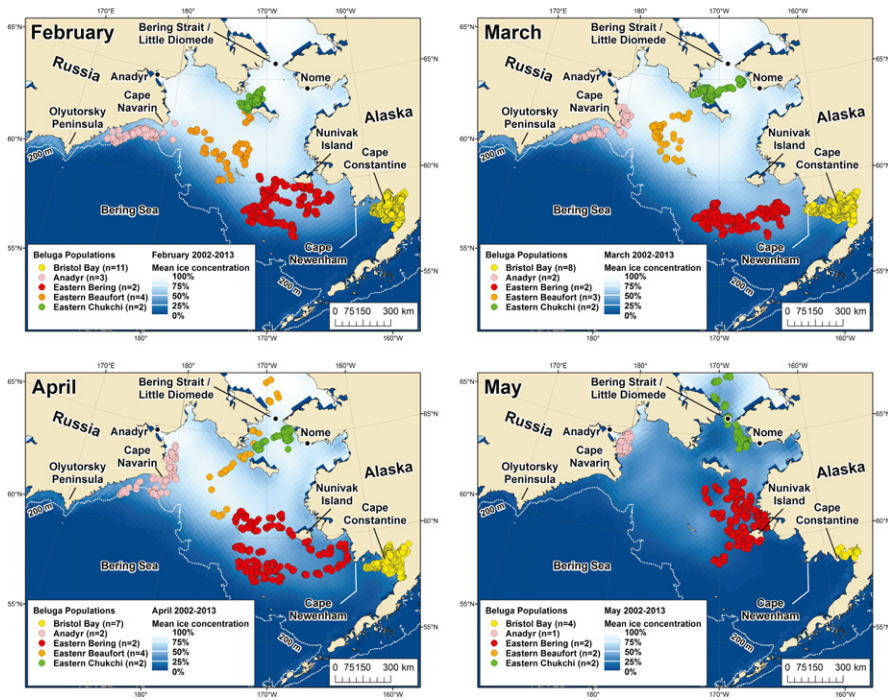


Figure 3. Beluga whale locations by population and month, February–May, all years pooled. Sea ice concentrations are Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data available at the National Snow and Ice Data Center (<https://nsidc.org/>). Concentration data were averaged by month during the study period (February 2002–May 2013).

animals made large loops, returning to the vicinity of Nunivak Island in May. One returned to Norton Sound on 12 June 2013 and the other returned on 13 June 2013.

Eastern Chukchi Sea (ECS) Population

Belugas from the eastern Chukchi Sea population were tagged at Point Lay in July. Six satellite tags transmitted long enough for them to pass south of Little Diomedede Island ($65^{\circ}45'N$) into the Bering Sea. Dates of entering the Bering Sea were between 8 November and 18 December (Appendix S2). Only one tag transmitted until the beluga reentered the Chukchi Sea; this beluga (EC07-01) exited the Bering Sea on 21 May 2015. One other tag transmitted into May, but was south of Being Strait when it stopped transmitting on 11 May 2013. The area used by ECS belugas was mainly limited to the Chirikov Basin, between St. Lawrence Island and Bering Strait, and Anadyr Strait, between St. Lawrence Island and the Russian mainland (Fig. 2, 3).

Eastern Beaufort Sea (EBS) Population

Six belugas from the EBS population, four tagged in 2004 and two in 2005, had satellite tags that transmitted from the Bering Sea (Appendix S2). Tags had a 6 d duty cycle, so dates of entry and exit from the Bering Sea are approximate unless the whale entered on a day when the tag was transmitting. Dates of entry ranged from 21

November to sometime between 6 and 18 December (Appendix S2). Four satellite tags transmitted until the whales reentered the Chukchi Sea the following spring. All four belugas left the Bering Sea sometime between 5 and 23 April (Appendix S2). The area used by the EBS belugas extended from the northwestern shore of St. Lawrence Island, south through Anadyr Strait, west to the Gulf of Anadyr, and southeast to St. Matthew Island (Fig. 2, 3).

Evidence for Traditional Wintering Areas

There were multiple years of tag data for four of the five populations. Prior to January, all belugas except those in the Bristol Bay population were still moving south into their winter ranges (Fig. 2). In April, EBS belugas began to migrate north (Fig. 3). January–March winter ranges, as represented by minimum convex polygons, were generally located within the same region for each population across years (Fig. 4). The distribution of Bristol Bay belugas was restricted to Bristol Bay in 2007, 2009, and 2013. ECS belugas were located in Anadyr Strait and the Chirikov Basin in both 2008 and 2013. EBS belugas ranged from Anadyr Strait, south to the region near St. Matthew Island in both 2005 and 2006. The distribution of Anadyr belugas was centered on Cape Navarin in 2002, 2007, and 2009; however, their distribution extended southwest past the Olyutorsky Peninsula in 2009. EB belugas were only tagged in 2013; hence, variation in the winter distribution cannot be addressed for this population.

Overlap of Wintering Areas

January–March winter ranges overlapped in two areas. First, beluga winter ranges overlapped for the ECS and EBS populations along the northwestern shore of St. Lawrence Island and in Anadyr Strait, between St. Lawrence Island and the Russian mainland (Fig. 4). Belugas in these populations were tagged in different years, so we cannot determine if they were in the same areas at the same time.

The second area of overlap included the ranges of the EB and Bristol Bay populations in outer Bristol Bay during the winter of 2012/2013. During January–March 2013, transmissions were received from tags on three Bristol Bay belugas and two EB belugas. During 17–23 January, one EB beluga was located east of Cape Newenham, in Bristol Bay (Fig. 5). This beluga did not travel east of Cape Constantine. At this time, the three tagged Bristol Bay belugas were all east of Cape Constantine. In February and March, Bristol Bay belugas ranged west of Cape Constantine, but did not pass west of Cape Newenham (Fig. 5). Hence, locations for these two populations overlapped in space, but not in time. Neither population ranged south of the marginal ice edge, defined here as ice concentrations between 15%–80%.

DISCUSSION

We found that satellite tagged belugas from all five populations either remained in, or moved into, the Bering Sea and spent the winter there. These populations generally wintered in different parts of the Bering Sea, and appeared to have winter ranges that were traditional and mostly exclusive. In a year when data were collected from a small number of tagged animals from two different populations that did overlap in space, they did not overlap in time. Our sample sizes were small for all

populations except the Bristol Bay population, thus we expect that the winter range for each population (Fig. 4) is likely larger and more variable than what we observed, leading to more overlap.

The juxtaposition of January–March winter ranges corresponds with observed patterns of genetic differentiation observed by O’Corry-Crowe *et al.* (1997, 2002, 2010). Breeding typically occurs in March and April, when belugas from the Bering, Chukchi, and Beaufort Seas are all still in the Bering Sea (Seaman and Burns 1981, Suydam 2009), and gene flow is predominantly mediated *via* male-biased dispersal or genetic exchange during the mating season (GO’C-C, personal observation). As such, the juxtaposition and degree of range overlap of population-specific wintering areas (Fig. 4) may reflect patterns of genetic exchange. Patterns within mitochondrial DNA markers suggest Bristol Bay belugas are more closely related to EB belugas than to other populations, while EB belugas are most closely related to Bristol Bay belugas, and more related to EBS belugas than to ECS belugas (GO’C-C, personal observation). This corresponds with our findings, as the winter and spring range of EB belugas is located in-between the ranges of Bristol Bay and EBS belugas (Fig. 4). Likewise, Meschersky *et al.* (2013) found that Anadyr belugas are more closely related to EBS belugas than ECS belugas. Again, this corresponds with our findings, as the winter and spring ranges of EBS belugas are located in-between the ranges of Anadyr and ECS belugas (Fig. 4). Comparisons of relatedness between Anadyr belugas and EB or Bristol Bay belugas have yet to be made.

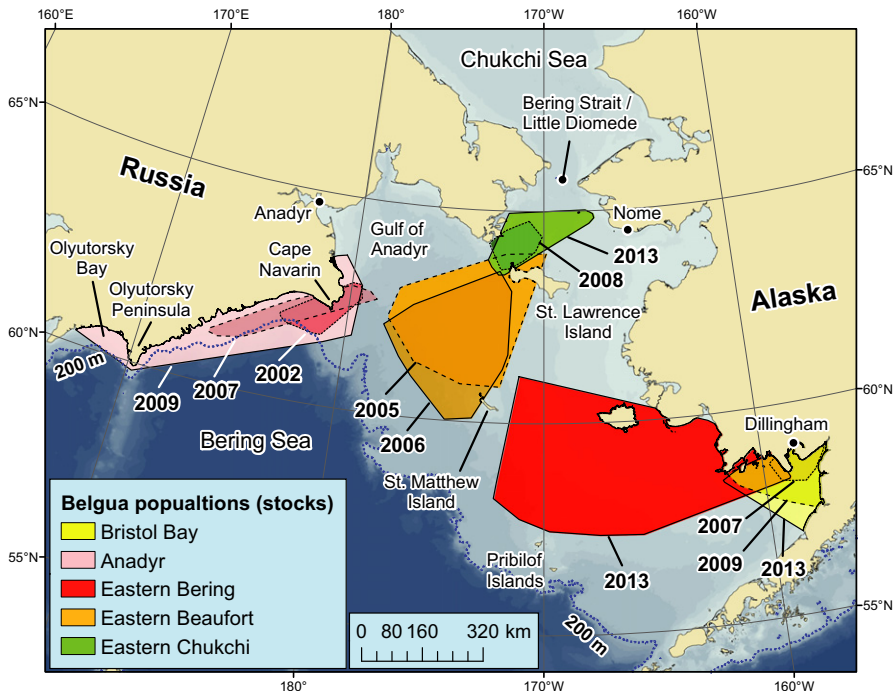


Figure 4. Winter ranges (minimum convex polygons) of beluga populations in the Bering Sea by year. Polygons are drawn using January–March locations and years are denoted by the degree of shading.

The location of population-specific wintering ranges likely results from belugas balancing a complex set of biological requirements, some of which are opposed to each other. The two obvious risks that need to be balanced are the risk of ice entrapment and the risk of predation. Belugas are known to sometimes become entrapped in sea ice and perish (e.g., Heide-Jørgensen *et al.* 2002, Ivashin and Shevlyagin 1987), which probably explains why eastern Beaufort Sea and eastern Chukchi Sea belugas migrate to the Bering Sea in winter, where pack ice is less concentrated, thinner, and more fractured. However, ice entrapment is also a risk in the Bering Sea. Two separate entrapment events were documented in 1984; the first near Little Diomede trapped at least 40 belugas (Lowry *et al.* 1987a) and the second in Senjavin Strait (Fig. 1), a confined location between an island and the Russian mainland, trapped 3,000–4,000 belugas (Ivashin and Shevlyagin 1987, Mymrin and Huntington 1999). Another event occurred in Senjavin Strait in 2011 when approximately 100 belugas were trapped (CNN 22 December 2011, BBC World News 15 December 2011).

We suspect that some regions of the Bering Sea have ice that is too consolidated for beluga whales. For example, the Gulf of Anadyr and Norton Sound generally contain consolidated pack ice (Brueggeman *et al.* 1987; Fig. 2, 3). These bodies of water are relatively enclosed by land, which increases the risk of entrapment because sea ice is not free to drift with the wind and will pile up and anchor along shorelines. Although belugas occupy both of these areas in summer, in winter they migrate south, closer to the ice edge where the pack is less concentrated (Fig. 2, 3) and there are no barriers for wind-driven ice to pile against. Although eastern Beaufort Sea and eastern Chukchi Sea belugas wintered north of the ice edge (Fig. 2, 3), they occupied a band of highly fractured sea ice that runs from Cape Navarin, northeast through Anadyr Strait (Brueggeman *et al.* 1987), where ice is relatively free to move north and south with winds. In contrast to the other populations, the summer range of Bristol Bay belugas is included within their winter range. Bristol Bay is located at the southern extent of the sea ice; open water occurs within Nushagak and Kvichak Bays throughout the winter (Citta *et al.* 2016) and the risk of entrapment is likely lower than where other populations summer (*i.e.*, the Chukchi and Beaufort Seas, Gulf of Anadyr, and Norton Sound).

However, belugas were not restricted to areas with recurrent polynyas. Polynyas, areas of open water within the sea ice, typically recur along the southern shores of St. Lawrence, St. Matthew, and Nunivak Islands, and along the northern shores of Norton Sound and the Gulf of Anadyr (see fig. 2.7 in Neibauer and Schell 1993). Some polynyas may not be safe for belugas to rely upon. For example, polynyas deep within the Gulf of Anadyr or Norton Sound may close when winds shift. However, belugas were not restricted to other large polynyas, such as the St. Lawrence Island polynya, suggesting belugas simply prefer other habitats, perhaps for feeding. To date, winter feeding is unstudied for these populations (see review in Quakenbush *et al.* 2015).

Although some ice conditions may pose an entrapment threat to belugas, winter ranges were generally located north of the marginal ice edge (Fig. 2, 3, 6). Belugas may remain north of the marginal ice edge to avoid predation by killer whales (*Orcinus orca*), which are known predators of belugas (e.g., Lowry *et al.* 1987b, Frost *et al.* 1992, Huntington 1999, Shelden *et al.* 2003). Killer whales occupy the Bering Sea in all seasons; in winter they are known to occur along and within the marginal ice zone, where pinnipeds are abundant (Leatherwood *et al.* 1983). Lowry *et al.* (1987b) reported killer whales in ice concentrations as high as 88% ($\frac{7}{8}$ coverage); however, sighted whales were generally within 10 km of the ice edge. The fact that beluga

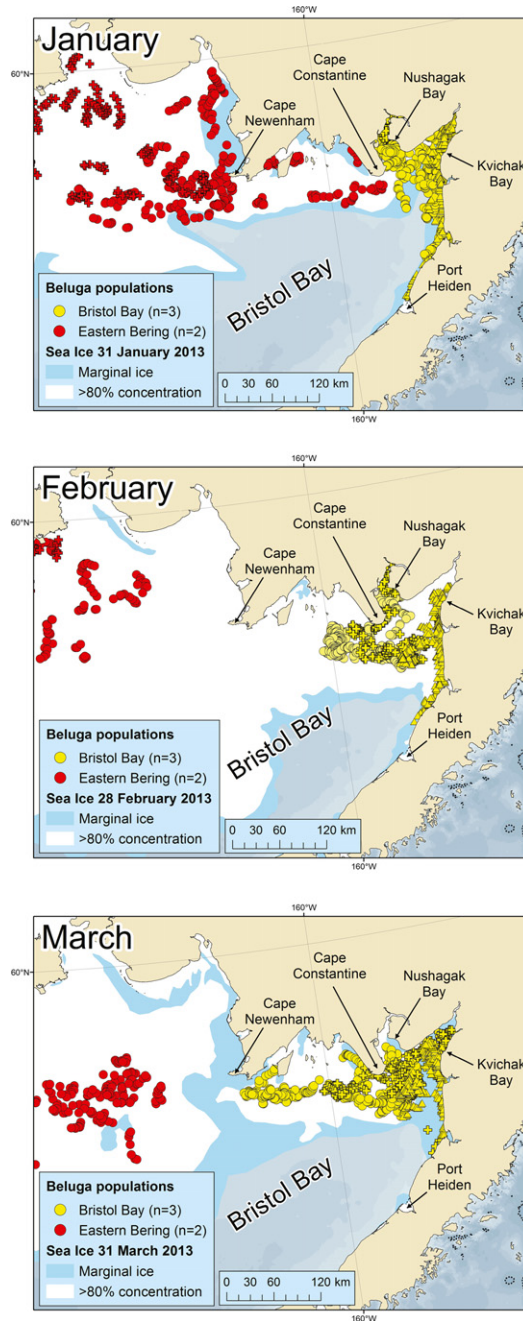


Figure 5. Beluga whale locations from December 2012 to March 2013 in the area of range overlap, between Cape Newenham and Cape Constantine. Colors denote populations and symbols denote individuals. Sea ice data concentration data are available at the National Ice Center (<http://www.natice.noaa.gov/>).

winter ranges generally were not located where polynyas occur has little to do with predation, as killer whales are not known to penetrate far enough into the ice to reach polynyas in the Arctic. Furthermore, if the risk of killer whale predation is limited to the marginal ice edge, predator avoidance does not explain why some beluga winter ranges are far north of the ice edge. Hence, while predation may explain why winter ranges are north of the ice edge, other factors such as ice conditions, food resources, or competition are likely more important within the ice pack.

Interestingly, tagged ECS belugas reached their winter ranges in the Chirikov Basin prior to when EBS belugas entered the Bering Sea. ECS belugas also exited the Bering Sea later than EBS belugas. As such, eastern Beaufort Sea belugas may pass by eastern Chukchi Sea belugas twice each winter; first when entering the Bering Sea for winter and again when leaving in the spring. Although the difference in timing may be an artifact of not having tags deployed in the same year, we know that eastern Beaufort Sea belugas bypass eastern Chukchi Sea belugas in autumn. In September, eastern Chukchi Sea belugas are located in the eastern Chukchi and western Beaufort Seas. At this time, eastern Beaufort Sea belugas travel north of these belugas to reach the western Chukchi Sea (*e.g.*, Hauser *et al.* 2014).

In April, when EBS belugas began to migrate north through the Chirikov Basin, ECS belugas shifted their distribution east, towards Nome, Alaska (Fig. 3). Few tags lasted long enough to transmit in April and only two tags were transmitting from each population at this time. April movements are inferred from one ECS beluga in 2007 and one in 2012. In both years, the ECS beluga moved into the eastern Chirikov Basin in April, towards Nome and away from the migration path of EBS belugas. Perhaps ECS belugas separate themselves from EBS belugas during their northward migration.

Other populations of belugas may also winter in the Bering Sea. The International Whaling Commission (IWC) tentatively recognizes belugas observed in the East Siberian Sea, in the Kolyma River (Kleinenberg *et al.* 1964) and near Wrangel Island (Belikov and Boltunov 2002; Solovyev *et al.* 2012), as a separate population (IWC 2000). It is possible, however, that belugas in the East Siberian Sea belong to the eastern Chukchi Sea or eastern Beaufort Sea populations. Belugas also once commonly entered Kotzebue Sound in summer (Frost and Lowry 1990) and these animals were genetically distinct from the other described populations (O’Corry-Crowe *et al.* 2002); it is unknown whether they constitute a separate Kotzebue Sound population, or belong to yet another, unknown population. If there are other populations in the Bering Sea that are north of the ice edge with exclusive ranges, it is unclear where they could be located. The areas east of St. Lawrence Island and south of St. Matthew Island are the only regions not already known to be occupied by belugas. The area south of St. Matthew is often not covered by sea ice in winter (Fig. 2, 3) and may not be suitable winter habitat if belugas prefer to remain north of the marginal ice zone.

Beluga populations appear to have traditional wintering areas that may be mostly exclusive. If this is the case, logical questions include how and why separate wintering ranges developed and how are they maintained. None of the winter or summer habitats these populations use were available during the last glacial maximum, when sea level was lower and the continental shelf was exposed (see fig. 1 in O’Corry-Crowe 2008). Bering Strait flooded approximately 11,000 YBP (Elias *et al.* 1996), opening habitat for beluga whales in the northern Bering, Chukchi, and Beaufort Seas. How belugas colonized newly available habitat likely has implications for the modern distribution of beluga whales. The maintenance of discrete summering areas is thought to be due to maternally directed philopatry (*e.g.*, Brown Gladden *et al.* 1997,

O'Corry-Crowe *et al.* 2002, Colbeck *et al.* 2012) and this also almost certainly plays a role in the maintenance of wintering areas.

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LITERATURE CITED

- Allen, B. M., and R. P. Angliss. 2014. Beluga whale (*Delphinapterus leucas*): Bristol Bay stock. NOAA Stock Assessment Report NOAA-TM-AFSC-301. 5 pp.
- Belikov, S. E., and A. N. Boltunov. 2002. Distribution and migrations of cetaceans in the Russian Arctic according to observations from aerial ice reconnaissance. Pages 69–86 in M. P. Heide-Jørgensen and Ø. Wiig, eds. Belugas in the North Atlantic and Russian Arctic. The North Atlantic Marine Mammal Commission, Tromsø, Norway.

- Braham, H. W., B. D. Krogman and G. M. Carroll. 1984. Bowhead and white whale migration, distribution, and abundance in the Bering, Chukchi, and Beaufort seas, 1975–78. U.S. Department of Commerce, NOAA Technical Report NFMS SSRF-778. 39 pp.
- Brown Gladden, J. G., M. M. Ferguson and J. W. Clayton. 1997. Matriarchal genetic population structure of North American beluga whales *Delphinapterus leucas* (Cetacea: Monodontidae). *Molecular Ecology* 6:1033–1046.
- Brueggeman, J. J., B. D. Webster, R. Grotefendt and D. G. Chapman. 1987. Monitoring of the winter presence of bowhead whales in the Navarin Basin through association with sea ice. Report for the U.S. Minerals Management Service by Envirosphere Company. OCS Study MSS 87-0028. 208 pp.
- Citta, J. J., L. T. Quakenbush, K. J. Frost, L. Lowry, R. C. Hobbs, and H. Aderman. 2016. Movements of beluga whales (*Delphinapterus leucas*) in Bristol Bay, Alaska. *Marine Mammal Science*. doi: 10.1111/mms.12337.
- Colbeck, G. J., P. Duchesne, L. D. Postma, V. Lesage, M. O. Hammill and J. Turgeon. 2012. Groups of related belugas (*Delphinapterus leucas*) travel together during their seasonal migrations in and around Hudson Bay. *Proceedings of the Royal Society B* 280:2012252.
- Elias, S. A., S. K. Short, C. H. Nelson and H. H. Birks. 1996. Life and times of the Bering land bridge. *Nature* 382:60–63.
- Fancy, S. G., L. F. Pank, D. C. Douglas, C. H. Curby, G. W. Garner, S. C. Amstrup and W. L. Regelin. 1988. Satellite telemetry: A new tool for wildlife research and management. Resource Publication 172. U. S. Fish and Wildlife Service, Washington, DC. 54 pp.
- Fraker, M. A. 1979. Spring migration of bowhead (*Balaena mysticetus*) and white whales (*Delphinapterus leucas*) in the Beaufort Sea. Canadian Fisheries and Marine Service Technical Report No. 859. 36 pp.
- Frost, K. J., and L. F. Lowry. 1990. Distribution, abundance, and movements of beluga whales, *Delphinapterus leucas*, in coastal waters of western Alaska. *Canadian Bulletin of Fisheries and Aquatic Sciences* 224:39–57.
- Frost, K. J., R. B. Russell and L. F. Lowry. 1992. Killer whales, *Orcinus orca*, in the southeastern Bering Sea: Recent sightings and predation on other marine mammals. *Marine Mammal Science* 8:110–119.
- Harwood, L. A., S. Innes, P. Norton and M. C. S. Kingsley. 1996. Distribution and abundance of beluga whales in the Mackenzie estuary, southeast Beaufort Sea, and west Amundsen Gulf during late July 1992. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2262–2273.
- Hauser, D. W. W., K. L. Laidre, R. S. Suydam and P. R. Richard. 2014. Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*). *Polar Biology* 37:1171–1183.
- Heide-Jørgensen, M. P., P. Richard, M. Ramsay and S. Akeagok. 2002. Three recent ice entrapments of Arctic cetaceans in West Greenland and the eastern Canadian High Arctic. Pages 143–148 in M. P. Heide-Jørgensen and Ø. Wiig, eds. Belugas in the North Atlantic and Russian Arctic. The North Atlantic Marine Mammal Commission, Tromsø, Norway.
- Hobbs, R., D. Litovka and G. O’Corry-Crowe. 2007. Bering sea wintering grounds of beluga whales. NPRB Project 324 Final Report, Anchorage, Alaska. Available at http://doc.nprb.org/web/03_prjs/r0324_Final_report-revised.pdf.
- Huntington, H. P. 1999. Traditional knowledge of the ecology of beluga whales (*Delphinapterus leucas*) in the eastern Chukchi and northern Bering seas, Alaska. *Arctic* 52:49–61.
- Ivashin, M. V., and K. V. Shevlyagin. 1987. The white whale (*Delphinapterus leucas* Pallas, 1776): Entrapment and escape in the ice of Senjavin Strait, U.S.S.R. Report of the International Whaling Commission 37:357–359.

- IWC (International Whaling Commission). 2000. Report of the Scientific Committee from its Annual Meeting 3–15 May 1999 in Grenada. *Journal of Cetacean Research and Management (Supplement)* 2:235–252.
- Kleinenberg, S. E., A. V. Yablokov, V. M. Bel'kovich and M. N. Tarasevich. 1964. Beluga (*Delphinapterus leucas*): Investigation of the species. Akademiya Nauk SSSR, Moscow. Translated from Russian by Israel Program for Scientific Translation, Jerusalem 1969. 376 pp.
- Laidre, K. L., H. Stern, K. M. Kovacs, *et al.* 2015. Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology* 29:724–737.
- Leatherwood, S., A. E. Bowles and R. R. Reeves. 1983. Aerial surveys of marine mammals in the southeastern Bering Sea. U.S. Department of Commerce, NOAA, OCSEAP Final Report 42:147–490.
- Lowry, L. F., J. J. Burns and R. R. Nelson. 1987*a*. Polar bear predation on beluga whales in the Bering and Chukchi seas. *Canadian Field-Naturalist* 101:141–146.
- Lowry, L. F., R. R. Nelson and K. J. Frost. 1987*b*. Observations of killer whales, *Orcinus orca*, in western Alaska: Sightings, strandings, and predation on other marine mammals. *Canadian Field-Naturalist* 101:6–12.
- Luque, S. P., and S. H. Ferguson. 2010. Age structure, growth, mortality, and density of belugas (*Delphinapterus leucas*) in the Canadian Arctic: Responses to environment? *Polar Biology* 33:163–178.
- Lydersen, C., A. R. Martin, K. M. Kovacs and I. Gjertz. 2001. Summer and autumn movements of white whales (*Delphinapterus leucas*) in Svalbard, Norway. *Marine Ecology Progress Series* 219:265–274.
- McConnell, B. J., C. Chambers and M. A. Fedak. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science* 4:393–398.
- Meschersky, I. G., O. V. Shpak, D. I. Litovka, D. M. Glazov, E. A. Borisova and V. V. Rozhnov. 2013. A genetic analysis of the beluga whale *Delphinapterus leucas* (Cetacea: Monodontidae) from summer aggregations in the Russian Far East. *Russian Journal of Marine Biology* 39:125–135.
- Mymrin, N. I., and H. P. Huntington. 1999. Traditional knowledge of the ecology of beluga whales (*Delphinapterus leucas*) in the northern Bering Sea, Chukotka, Russia. *Arctic* 52:62–70.
- Niebauer, H. J., and D. M. Schell. 1993. Physical environment of the Bering Sea population. Pages 23–43 in J. J. Burns, J. H. Montague and C. J. Cowles, eds. *The bowhead whale*, Special Publication Number 2, The Society for Marine Mammalogy.
- O'Corry-Crowe, G. 2008. Climate change and the molecular ecology of Arctic marine mammals. *Ecological Applications* 18:56–76 (supplement).
- O'Corry-Crowe, G. M., R. S. Suydam, A. Rosenberg, K. J. Frost and A. E. Dizon. 1997. Phylogeography, population structure and dispersal patterns of the beluga whale *Delphinapterus leucas* in the western Nearctic revealed by mitochondrial DNA. *Molecular Ecology* 6:955–970.
- O'Corry-Crowe, G. M., A. E. Dizon, R. S. Suydam and L. F. Lowry. 2002. Molecular genetic studies of population structure and movement patterns in a migratory species: The beluga whale (*Delphinapterus leucas*) in the western Nearctic. Pages 53–64 in C. J. Pfeiffer, ed. *Molecular and cell biology of marine mammals*. Krieger Publishing Co., Malabar, FL.
- O'Corry-Crowe, G. M., C. Lydersen, M. P. Heide-Jørgensen, L. Hansen, L. M. Mukhametov, O. Dove and K. M. Kovacs. 2010. Population genetic structure and evolutionary history of North Atlantic beluga whales (*Delphinapterus leucas*) from West Greenland, Svalbard and the White Sea. *Polar Biology* 33:1179–1194.

- Orr, J. R., D. J. Aubin, P. R. Richard and M. P. Heide-Jørgensen. 1998. Recapture of belugas, *Delphinapterus leucas*, tagged in the Canadian Arctic. *Marine Mammal Science* 14:829–834.
- Quakenbush, L. T., R. S. Suydam, A. L. Bryan, L. F. Lowry, K. J. Frost and B. A. Mahoney. 2015. Diet of beluga whales, *Delphinapterus leucas*, in Alaska from stomach contents, March–November. *Marine Fisheries Review* 77:70–84.
- Richard, P. R., A. R. Martin and J. R. Orr. 2001. Summer and autumn movements of belugas of the eastern Beaufort Sea stock. *Arctic* 54:223–236.
- Rodgers, A. R. 2001. Recent telemetry technology. Pages 79–121 in J. J. Millspaugh and J. M. Marzluff, eds. *Radio tracking and animal populations*. Academic Press, San Diego, CA.
- Seaman, G. A., and J. J. Burns. 1981. Preliminary results of recent studies of belukhas in Alaskan waters. Report of the International Whaling Commission 31:567–574.
- Shelden, K. E. W., D. J. Rugh, B. A. Mahoney and M. E. Dahlheim. 2003. Killer whale predation on belugas in Cook Inlet, Alaska: Implications for a depleted population. *Marine Mammal Science* 19:529–544.
- Smith, T. G., and A. R. Martin. 1994. Distribution and movements of belugas, *Delphinapterus leucas*, in the Canadian High Arctic. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1653–1663.
- Solovyev, B. A., N. G. Platonov, D. M. Glazov, O. V. Shpak and V. V. Rozhnov. 2012. Distribution of beluga whales (*Delphinapterus leucas*) in the Russian Arctic seas according to the results of expedition aboard RV Mikhail Somov, September–November 2010. *Biology Bulletin* 39:65–658.
- Suydam, R. S. 2009. Age, growth, reproduction, and movements of beluga whales (*Delphinapterus leucas*) from the eastern Chukchi Sea. Ph.D. dissertation, University of Washington, Seattle, WA. 152 pp.
- Suydam, R. S., L. F. Lowry, K. J. Frost, G. M. O’Corry-Crowe and D. Pikkok, Jr. 2001. Satellite tracking of eastern Chukchi Sea beluga whales into the Arctic Ocean. *Arctic* 54:237–243.

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SUPPORTING INFORMATION

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Appendix S1. Belugas tagged with satellite-linked transmitters included in this study. ID numbers are a composite of the population abbreviation (BB = Bristol Bay, AN = Anadyr, EB = Eastern Bering Sea, ECS = Eastern Chukchi Sea, and EBS = Eastern Beaufort Sea), the two digit year, and the order of tagging. For example, BB03-05 is the fifth Bristol Bay beluga tagged in 2003. Duty cycle denotes the hours and days the transmitters were programmed to transmit.

Appendix S2. Dates beluga whales entered and exited the Bering Sea for the two stocks that summer north of Bering Strait. All whales with active transmitters in October are shown. Some tags ceased transmitting prior to entering the Bering Sea or prior to leaving the Bering Sea in spring. Due to how transmitter duty cycles were specified, the actual day Eastern Beaufort Sea belugas entered or exited the Bering Sea was often unknown. Hence, dates are shown as a range of possible days. See Appendix S1 for transmitter specifications.