Decadal shifts in autumn migration timing by Pacific Arctic beluga whales are related to delayed annual sea ice formation

DONNA D. W. HAUSER[1,2], KRISTIN L. LAIDRE[1,2], KATHLEEN M. STAFFORD[3], HARRY L. STERN[2], ROBERT S. SUYDAM[4] and PIERRE R. RICHARD[5]

[1]School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98105, USA, [2]Polar Science Center, Applied Physics Laboratory, University of Washington, 1013 NE 40th Street, Seattle, WA 98105, USA, [3]Applied Physics Laboratory, University of Washington, Seattle, WA 98105, USA, [4]North Slope Borough, Department of Wildlife Management, PO Box 69, Barrow, AK 99723, USA, [5]Freshwater Institute, Fisheries & Oceans Canada, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

Abstract

Migrations are often influenced by seasonal environmental gradients that are increasingly being altered by climate change. The consequences of rapid changes in Arctic sea ice have the potential to affect migrations of a number of marine species whose timing is temporally matched to seasonal sea ice cover. This topic has not been investigated for Pacific Arctic beluga whales (*Delphinapterus leucas*) that follow matrilineally maintained autumn migrations in the waters around Alaska and Russia. For the sympatric Eastern Chukchi Sea ('Chukchi') and Eastern Beaufort Sea ('Beaufort') beluga populations, we examined changes in autumn migration timing as related to delayed regional sea ice freeze-up since the 1990s, using two independent data sources (satellite telemetry data and passive acoustics) for both populations. We compared dates of migration between 'early' (1993–2002) and 'late' (2004–2012) tagging periods. During the late tagging period, Chukchi belugas had significantly delayed migrations (by 2 to >4 weeks, depending on location) from the Beaufort and Chukchi seas. Spatial analyses also revealed that departure from Beaufort Sea foraging regions by Chukchi whales was postponed in the late period. Chukchi beluga autumn migration timing occurred significantly later as regional sea ice freeze-up timing became later in the Beaufort, Chukchi, and Bering seas. In contrast, Beaufort belugas did not shift migration timing between periods, nor was migration timing related to freeze-up timing, other than for southward migration at the Bering Strait. Passive acoustic data from 2008 to 2014 provided independent and supplementary support for delayed migration from the Beaufort Sea (4 day yr^{-1}) by Chukchi belugas. Here, we report the first phenological study examining beluga whale migrations within the context of their rapidly transforming Pacific Arctic ecosystem, suggesting flexible responses that may enable their persistence yet also complicate predictions of how belugas may fare in the future.

Keywords: Beaufort Sea, Bering Sea, cetacean, Chukchi Sea, climate change, foraging ecology, marine mammal, passive acoustics, phenology, satellite telemetry

Received 22 July 2016; revised version received 20 October 2016 and accepted 7 November 2016

Introduction

The evolution and maintenance of migratory behavior often represents a response to seasonal environmental gradients, and thus, climate change is expected to affect the frequency and magnitude of migratory behaviors (Cresswell *et al.*, 2011). However, migratory species are somewhat of a paradox when assessing potential vulnerability to climate change (Robinson *et al.*, 2009). On the one hand, migratory species are mobile, often characterized by populations exhibiting multiple migration strategies, and could be expected to readily adjust to changes in environmental suitability. Alternatively migrations could be innate behaviors or socially maintained (Colbeck *et al.*, 2013). Therefore, migratory species may be adapted to and dependent on predictable habitat of functional importance (e.g., for breeding, foraging, or molting) during the migration cycle, which may be differentially affected by climate change. Several life history characteristics of migratory individuals could be affected by climate-related physical changes such as timing, distance, and direction/route of migration as well as the propensity to migrate (Shuter *et al.*, 2011; Bailleul *et al.*, 2012b; Seebacher & Post, 2015).

Arctic marine ecosystems are experiencing some of the most prominent signals of global climate change, demonstrated as unprecedented rates of seasonal ice

Correspondence: Donna D. W. Hauser, tel. +1 907 474 1811, fax +1 206 616 3142, e-mail: dhauser@uw.edu

loss occurring over broad spatial scales (Serreze & Stroeve, 2015). Sea ice extent, volume, and duration of cover have declined on a pan-Arctic scale, regional variability not withstanding (Stroeve *et al.*, 2012; Barnhart *et al.*, 2016). There have been shifts in lower-level productivity, associated with changing physical conditions in Arctic marine ecosystems (e.g., Grebmeier, 2012), yet limited research has been conducted to consider the implications of physical changes at the highest trophic levels (Wassmann *et al.*, 2011). In particular, the duration of the open-water season has significantly increased in nearly all Arctic regions, and the timing of annual ice retreat and advance is thought to particularly affect Arctic marine mammals (Laidre *et al.*, 2015). Arctic marine mammals are long-lived with low reproductive rates and have life histories, reproduction, and foraging strategies matched temporally to sea ice conditions, which can make them particularly susceptible to broad-scale, sudden, and unidirectional changes (Laidre *et al.*, 2008; Kovacs *et al.*, 2011). Impacts of sea ice loss are more direct for species dependent on ice as a platform for specialized feeding, reproduction, or resting (e.g., polar bears *Ursus maritimus*, Cherry *et al.*, 2013; Rode *et al.*, 2015). It is less clear what changing environments mean for Arctic cetaceans indirectly associated with sea ice habitat via shifts in prey productivity and community structure that result from changing sea ice conditions (Moore & Huntington, 2008). Changes in distribution and timing of migration are the most anticipated types of responses for these ice-associated cetaceans whose movements are temporally coordinated to annual sea ice cycles (Gilg *et al.*, 2012).

The rate and intensity of sea ice changes have been particularly pronounced since the 1990s in the Pacific Arctic (Maslanik *et al.*, 2011; Frey *et al.*, 2015; Wood *et al.*, 2015), which could affect two migratory populations of beluga whales (*Delphinapterus leucas*), the Eastern Chukchi Sea ('Chukchi') and Eastern Beaufort Sea ('Beaufort') populations. Chukchi and Beaufort belugas migrate thousands of kilometers during the open-water season from the sub-Arctic northern Bering Sea to the seasonally productive high Arctic Chukchi and Beaufort seas (Richard *et al.*, 2001; Suydam *et al.*, 2001), which have each experienced significant increases in the average open-water season over the last three decades (~13 and 15 days per decade, respectively, Laidre *et al.*, 2015). Traditional knowledge, aerial surveys, telemetry data, and biological sampling indicate that each genetically distinct population is philopatric to discrete summering areas (Frost & Lowry, 1990; O'Corry-Crowe *et al.*, 1997; Harwood & Smith, 2002; Huntington *et al.*, 2004; Hauser *et al.*, 2014), where the annual retreat and advance of dense pack ice presumably affects the ability of Chukchi and Beaufort belugas to safely access summer foraging habitat in the Chukchi and Beaufort seas (Moore, 2000; Garland *et al.*, 2015a; Hauser *et al.*, 2015).

Beluga whales exhibit predictable migration behaviors that have been passed down matrilineally (Colbeck *et al.*, 2013). It is unknown whether Pacific Arctic belugas will adjust migrations as sea ice shifts, or to what extent beluga migrations will respond to environmental changes as the behaviors are learned from their mothers. We use two independent types of data (telemetry and passive acoustics) to examine potential changes in Chukchi and Beaufort beluga autumn migration timing associated with changes in the timing of seasonal ice cover. Autumn sea ice advance (or 'freeze-up') in the Chukchi and Beaufort seas has occurred an average of at least 1 week later each decade over 1979 to 2013 (Fig. S1; Laidre *et al.*, 2015). Assuming that freeze-up timing, in areas where whales are migrating to or from, affects access to Chukchi and Beaufort sea foraging regions, we predict that west and southward autumn migration is related to the timing of sea ice freeze-up. If regional sea ice timing is an important factor determining timing of beluga migration, we hypothesize that migration timing would shift later as freeze-up occurs later in more recent years.

Materials and methods

Study area and migratory 'passage boundaries'

Chukchi and Beaufort beluga whales make extensive migrations between winter areas in the northern Bering Sea and summer foraging regions in the Pacific Arctic (Hauser *et al.*, 2015). Belugas pass several key latitudes and longitudes during autumn that are relevant to the management and biology of each population, referred to here as 'passage boundaries', on return trips to the Bering Sea (Fig. 1). First, Beaufort belugas commence westward autumn migration in September, traversing and exiting the Beaufort Sea approximately 1 month earlier than Chukchi whales (Richard *et al.*, 2001; Hauser *et al.*, 2014). We defined initiation of migration for Beaufort belugas when they cross 141° W, the northward extension of the United States–Canada border that also closely matches the western edge of the Beaufort beluga July–August summer home range (Hauser *et al.*, 2014). Beaufort whales remain in the Chukchi Sea before both populations typically commence southward migration around November (Hauser *et al.*, 2014). We considered three additional passage boundaries relevant to both beluga populations that correspond to exits from the Beaufort and Chukchi seas (157° W and 65.9° N, respectively) and final autumn movement past 70° N where whales must turn south in the Chukchi Sea (Fig. 1, Table 1). Passage boundaries for exit from the Beaufort and Chukchi seas correspond to regional sea ice boundaries (see 'Comparisons with regional sea ice timing'). Exit from the Chukchi Sea represents passage into the Bering Strait.
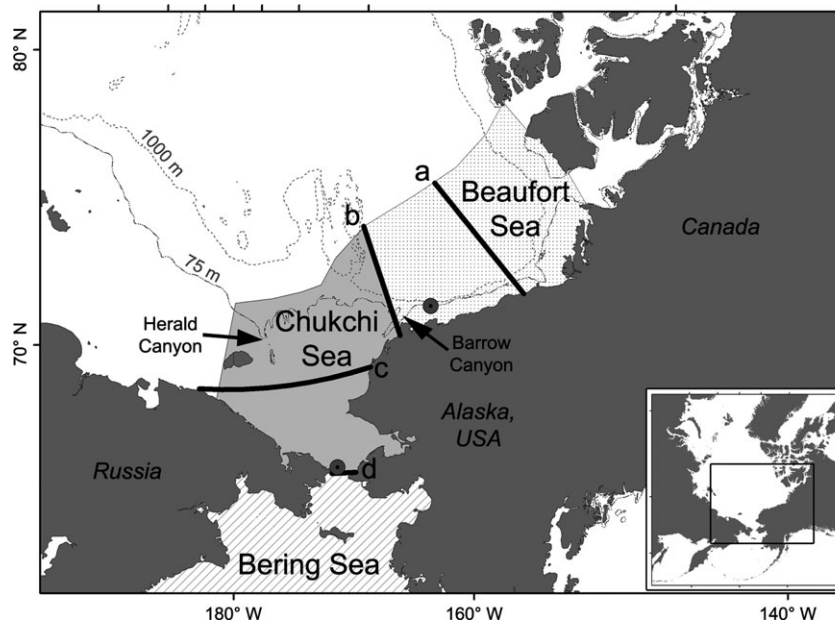
Fig. 1 Map of the study area, including hydrophone locations (gray dots), passage boundaries (black lines labeled a-d at 141° W, 157° W, 70° N, and 65.9° N, respectively), sea ice regions (i.e., the Bering Sea, Chukchi Sea, and Beaufort Sea), and place names mentioned in the text. Passage at (d) corresponds to the Bering Strait.

Table 1 Passage boundaries transited by tagged beluga whales without return in a given year, and comparisons between early and late period sample sizes, median (and range) migration day of year, and overall number of days between median dates (and results of Kruskal–Wallis rank sum test). Significant statistical relationships ($P < 0.05$) are bolded

Passage boundary	No. of tagged whales in early, late periods	Median migration day of year (range) in early, late periods	Days between median dates (late–early)
Eastern Chukchi Sea belugas			
Exit Beaufort Sea (first day west of 157° W)	4, 7	279.5 (279–286), 312.5 (289–324)	**+33** ($\chi^2 = 6.63$, df = 1, $P = 0.010$)
Commence southward migration (last day north of 70° N)	4, 6	295.5 (286–299), 316.5 (311–328)	**+21** ($\chi^2 = 6.55$, df = 1, $P = 0.011$)
Enter Bering Sea (first day south of Bering Strait, 65.9° N)	3, 4	316.0 (313–318), 330.0 (321–352)	**+14** ($\chi^2 = 4.50$, df = 1, $P = 0.034$)
Eastern Beaufort Sea belugas			
Exit Canada (first day west of 141° W)	12, 7	252.0 (214–264), 246.0 (246–262)	−6 ($\chi^2 = 0.30$, df = 1, $P = 0.584$)
Exit Beaufort Sea (first day west of 157° W)	11, 7	261.0 (221–277), 253.0 (246–271)	−8 ($\chi^2 = 0.60$, df = 1, $P = 0.440$)
Commence southward migration (last day north of 70° N)	8, 7	290.0 (279–303), 292.0 (279–295)	+2 ($\chi^2 = 0.09$, df = 1, $P = 0.770$)
Enter Bering Sea (first day south of Bering Strait, 65.9° N)	0, 6	N/A, 344.5 (326–347)	N/A

Telemetry data

We used location data from satellite-linked data recorders attached to Chukchi and Beaufort beluga whales near Point Lay, Alaska and the Mackenzie River Estuary, Canada, respectively (Table S1; Orr *et al.*, 2001; Richard *et al.*, 2001; Suydam, 2009; Suydam *et al.*, 2001). Biopsies taken in June and July of tagged whales at these sites correspond to samples from subsistence-harvested belugas collected since ~1990, indicating that Chukchi and Beaufort belugas are genetically distinct (O'Corry-Crowe *et al.*, 1997). We used data from Chukchi belugas from 1998 to 2012, including one male ('B07-1') in 2007 that provided locations through the 2008 autumn migration. We used data from Beaufort whales tagged between 1993 and 2005. Chukchi tags transmitted continuously, but Beaufort

tags were programmed to transmit either continuously or according to 1- to 6-days duty cycles (Richard *et al.*, 2001). We used a continuous correlated random walk model to standardize the frequency of locations by estimating daily geographic locations for each whale, which were based on observed satellite locations and their associated spatial error, using the 'crawl' package in R (Johnson *et al.*, 2008).

We compared telemetry data for each population among clustered years when tagging occurred to consider temporal changes in distribution and migration timing. These periods generally correspond to differing sea ice conditions experienced in the 1990s ('early tagging period': 1993–2002) and 2000s ('late tagging period': 2004–2012; Fig. S1). We note that the early tagging period of the Beaufort population (1993–1997) precedes the early tagging period of the Chukchi population (1998–2002), and the late tagging period of the Beaufort population (2004–2005) precedes the late tagging period of the Chukchi population (2007–2012; Table S1). Therefore, in comparing autumn migration timing vs. sea ice freeze-up dates between the two populations, some assurance is needed that the results are not confounded by the different observation periods and indeed distinct sea ice conditions were experienced between periods. In a recent analysis, Close *et al.* (2015) used satellite passive microwave sea ice concentration data (1979–2013) to identify areas of the Arctic Ocean where the seasonal mean sea ice concentration (SIC) exhibits 'breakpoint' behavior, such as stable SIC before a certain year and then declining SIC after that year. Most of the Beaufort and Chukchi seas exhibit such breakpoint behavior in summer (July–September) and autumn (October–December), with the transition year in the autumn SIC time series identified as 2001 ($\pm$3 years). This definitively puts the late tagging periods of both beluga populations in the post-transition regime of declining sea ice. There are several other physical and biological signals of a new Pacific Arctic ecosystem state commencing around 2004 besides (and in association with) ice loss (Moore & Stabeno, 2015; Wood *et al.*, 2015), lending weight to the idea that a transition occurred shortly before that time. Therefore, we suggest that our results are not an artifact of the sampling scheme and that it is possible to compare autumn migration timing between the two populations, because both early sampling periods are in the pre-transition sea ice regime and both late sampling periods are in the post-transition regime.

We estimated monthly ranges and concentration areas to examine the autumn spatial distribution of each population between periods. For each period, we estimated the monthly utilization distribution of each population during September–November using bivariate normal kernel density estimation (Worton, 1989). We used the 'kde' tool in the Geospatial Modeling Environment (spatialecology.com/gme), which is based on the 'ks' package in R (Duong, 2007). We selected bandwidths using least-squares cross-validation and defined monthly ranges and concentration areas as the 90% and 50% probability contours of the estimated utilization distribution, respectively (Börger *et al.*, 2006). We also estimated monthly geographic mean centers (Haining, 2003) for each period, measuring the Euclidean distance between monthly mean centers to evaluate geographic displacement of tagged whales in the early versus late period.

We identified the day of the year when tagged whales transited each passage boundary without return. The sample size of whales crossing each passage boundary decreased the further west and south each boundary occurred in the autumn migration path as tags began to fail (i.e., batteries failed, tags detached, antennae broke; Table 1). We excluded a few cases when passage dates were also the date of last transmission, so we could not definitively determine final passage of the whale. We evaluated differences in migration timing between early and late periods for each population and at each passage boundary using Kruskal–Wallis rank sum tests.

Passive acoustic data

We deployed hydrophone packages (Multi-électronique Aural M2) on moorings in the western Beaufort Sea (71.4° N, 152° W) and just north of Bering Strait (66.3° N, 168.95° W) to monitor vocalizing marine mammals and ambient noise (Fig. 1). The Beaufort Sea instrument recorded year-round from September 2008 through July 2013 on a 30% duty cycle (the first 9 min every half hour). The Bering Strait instrument recorded autumn data (September through December) from 2009 through 2014 on a 25% duty cycle, such that data were recorded for the first 15 min of every hour. We sampled acoustic data at 8192 Hz for an effective monitored bandwidth of 10–4096 Hz, which is sufficient to record the whistles and pulsed signals of beluga whales, but not higher frequency echolocation signals. We visually examined spectrograms of each data file for the presence of beluga whale calls, and the number of hours per day with calls was determined to examine seasonal occurrence (Sjare & Smith, 1986). The detection range for beluga whale calls will vary with ambient noise levels (Miller, 2006) but is estimated to range from 5 to 15 km based on measurements of belugas from Saguenay Fjord, Canada, and comparative distances for other odontocetes that produce similar sounds (Miller, 2006; Gervaise *et al.*, 2012).

Beluga migration at the Beaufort Sea and Bering Strait mooring locations occurred in pulses over the duration of the open-water and autumn seasons, so we considered the distribution of dates over which beluga vocalizations were detected (see Fig. S2). It is not currently possible to determine population identity from vocalizations (but see Garland *et al.*, 2015b), but we could assume beluga vocalizations observed after September at the Beaufort Sea location were characteristic of Chukchi belugas based on previous studies (Richard *et al.*, 2001; Suydam *et al.*, 2001; Hauser *et al.*, 2014; Garland *et al.*, 2015a; Stafford *et al.*, in press). We focused on the far right tail of the cumulative distribution of calling days to determine final migration date of Chukchi belugas out of the Beaufort Sea. Specifically, we identified the passage date for Chukchi belugas at the Beaufort Sea mooring as the 95% quantile of the cumulative distribution of days when vocalizations occurred after September 30 each year (Fig. S2). We assumed this passage date corresponds to the annual departure of Chukchi belugas from the Beaufort Sea.

It was not possible to differentiate population identity at the Bering Strait hydrophone where both populations overlap spatially in November (Hauser *et al.*, 2014), moving south from early November to mid-December (Citta *et al.*, 2016).

Belugas were detected at the Bering Strait hydrophone during autumn from early November to late December (Fig. S2). We examined the median date of days with beluga vocalizations during autumn each year, 2009–2014, to consider beluga migration timing at the Bering Strait hydrophone.

Comparisons with regional sea ice timing

The day of sea ice advance ('freeze-up') each autumn, 1979–2013, has occurred significantly later in the Beaufort and Chukchi seas (7.8 and 7.0 days per decade, respectively; Laidre *et al.*, 2015), although there were not significant trends in the Bering Sea (Fig. S1). We examined the relationship between autumn migration timing (i.e., passage dates from both telemetry and acoustic data) and regional sea ice timing using the day of freeze-up, determined in Laidre *et al.* (2015), for each year in the Bering, Chukchi, and Beaufort sea regions (Fig. 1). Briefly, the daily sea ice area for each year (1979–2014) and region was estimated from SSM/I satellite-derived sea ice products (Cavalieri *et al.*, 1996, updated yearly). We defined the day of sea ice advance in each region as the day each autumn when the area of sea ice first exceeded half the area of the region. We used least-squares regression to compare the day of migration each year to the day of sea ice freeze-up in the Bering, Chukchi, and Beaufort seas.

Results

Migration phenology of tagged belugas

A total of 65 Chukchi and Beaufort belugas were tagged between 1993 and 2012, but the number of tagged belugas whose tags transmitted through November or that crossed each passage boundary was variable due to the timing of tag failure (Tables 1 and S1). The autumn distribution of monthly ranges, concentration areas, and mean centers was distinct for Chukchi belugas in the early compared with the late period (Fig. 2). Chukchi belugas in September, October, and November were distributed farther north and east in the late period than in the early period. In October, Chukchi belugas tagged in the late period remained near the Beaufort Sea continental slope compared with the October range of whales tagged in the early period that extended west- and southward in the Chukchi Sea. The displacement distance (based on Euclidean distance) between early and late period mean center locations was greatest for Chukchi belugas in October (549 km). The November range of Chukchi belugas tagged in the late period spanned from the Bering Strait to Beaufort Sea compared with the more compacted range focused in the Bering Strait for whales tagged in the early period; straight-line distance between mean centers was 454 km, although displacement including travel around land masses would be much greater. There was less variation in the distribution of autumn monthly ranges,

concentration areas, and mean centers for Beaufort belugas than Chukchi belugas (Fig. 2). The greatest difference in spatial distribution of Beaufort belugas occurred in September when whales tagged in the late period had a larger range that was concentrated farther west (mean centers separated by 280 km) than those in the early period. There was relatively limited separation in Beaufort beluga ranges, concentration areas, and mean centers (≤130 km) between periods during October and November.

Chukchi beluga migration timing occurred later in the autumn during 2007–2012 compared with the early period (i.e., 1998–2002) for all passage boundaries (Table 1). It was also positively correlated with the timing of sea ice advance (Table S2, Fig. 3). Specifically, the date of exit from the Beaufort Sea (157° W), commencement of southward migration (70° N), and passage into the Bering Strait (65.9° N) were consistently and significantly delayed in the late tagging period (median dates 14–33 days later) than the early tagging period (Table 1). For each of these passage boundaries, passage date was positively related to the date of sea ice freeze-up in the Beaufort, Chukchi, and Bering seas. Correlations between passage date and timing of regional freeze-up were best explained by the timing of freeze-up in the region whales were departing from rather than timing in regions whales were oriented toward.

In contrast, there were no changes in migration timing or correlations with regional freeze-up timing for Beaufort belugas between early (i.e., 1993–1997) and late (i.e., 2004–2005) tagging periods, other than correlation with regional freeze-up upon entrance into the Bering Strait (65.9° N; Tables 1 and S2, Fig. S3). There were no locations of Beaufort belugas south of Bering Strait in the early period to compare with those in the late period. However, the date of migration by late period whales at Bering Strait was significantly correlated with freeze-up timing in each sea ice region. Beaufort belugas also passed each location ahead of Chukchi belugas as expected from previous analyses (Hauser *et al.*, 2014), other than at Bering Strait. At Bering Strait, Beaufort belugas' median migration dates were ~2 weeks later than those of Chukchi belugas in the late period (Table 1).

Migration phenology of acoustically detected belugas

The 95% quantile date of beluga autumn passage, assumed to represent final departure from the Beaufort Sea by Chukchi belugas, occurred 4.1 days later each year (2008–2013) at the Beaufort Sea hydrophone, although the relationship was not statistically significant ($r^2 = 0.44$, $P = 0.15$; Fig. 4). The date of Chukchi
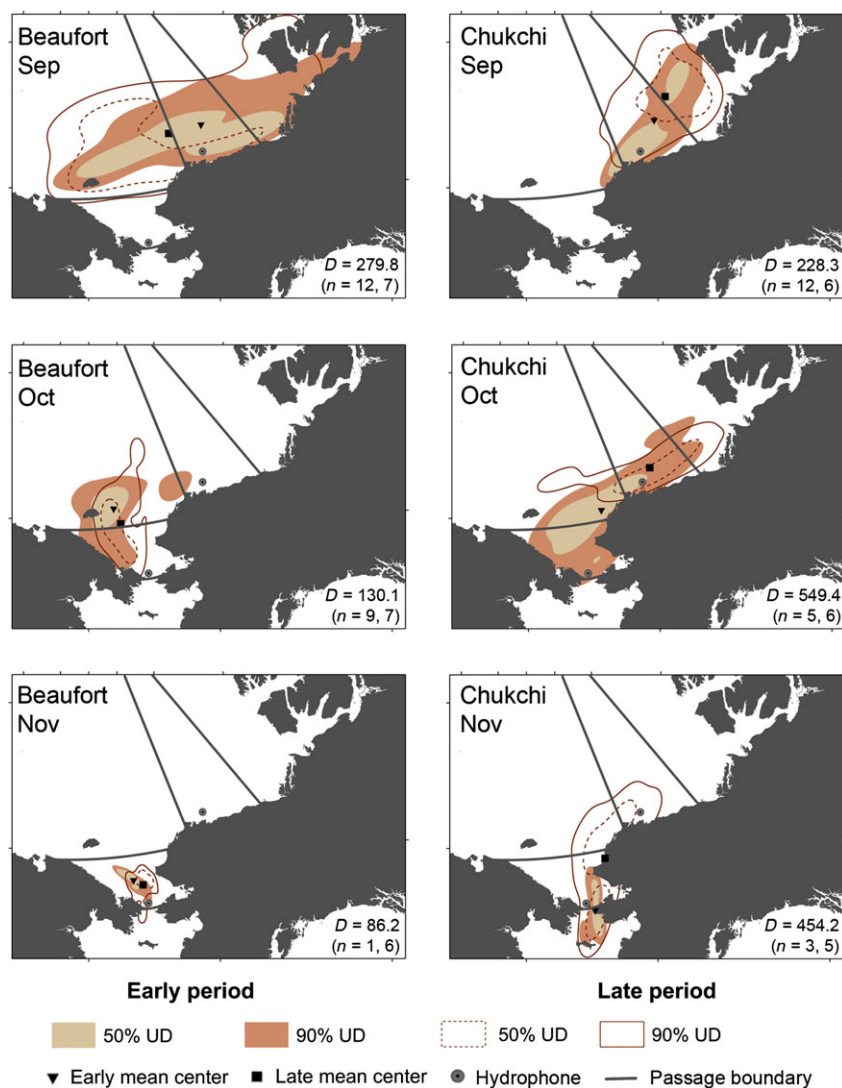
Fig. 2 Spatial distribution of autumn (September–November) monthly ranges (90% probability contour of the utilization distribution, UD), concentration areas (50% contour of the UD), and mean centers for tagged Chukchi and Beaufort beluga whales. Displacement (*D*, in km) between early and late mean center locations and the number of tagged whales (*n* = early, late period) are indicated in the lower right corner for each. [Colour figure can be viewed at wileyonlinelibrary.com]

beluga autumn passage was positively related to the date of Beaufort Sea freeze-up ($r^2 = 0.60$, $P = 0.07$; Fig. 4). Autumn passage date at the Beaufort Sea hydrophone was not related to the date of freeze-up in the Chukchi or Bering seas ($r^2 = 0.02$, $P = 0.77$ and $r^2 = 0.01$, $P = 0.85$, respectively).

The median date of beluga vocalizations at the Bering Strait hydrophone occurred 1.1 day later each year, from 2009 to 2014 ($r^2 = 0.10$, $P = 0.54$; Fig. 4). There were no strong relationships of median date with freeze-up date in the Chukchi or Beaufort seas ($r^2 = 0.12$, $P = 0.50$ and $r^2 = 0.30$, $P = 0.26$, respectively) although the strongest positive correlation occurred with Bering Sea freeze-up timing ($r^2 = 0.44$, $P = 0.15$; Fig. 4).

Discussion

Arctic ecosystems are experiencing some of the most profound and rapid changes on Earth, yet limited baselines have hindered assessments of impacts to regional marine mammal populations (Laidre *et al.*, 2015). Few studies have examined ice-related responses of Arctic cetaceans. Those that have primarily focused on regional shifts in distribution or changes in body condition of well-sampled populations (e.g., Heide-Jørgensen *et al.*, 2010, 2012; George *et al.*, 2015). In contrast, establishing a relationship of sea ice loss has been more forthcoming for ice-obligate Arctic pinnipeds and polar bears that require predictable ice cycles to match the
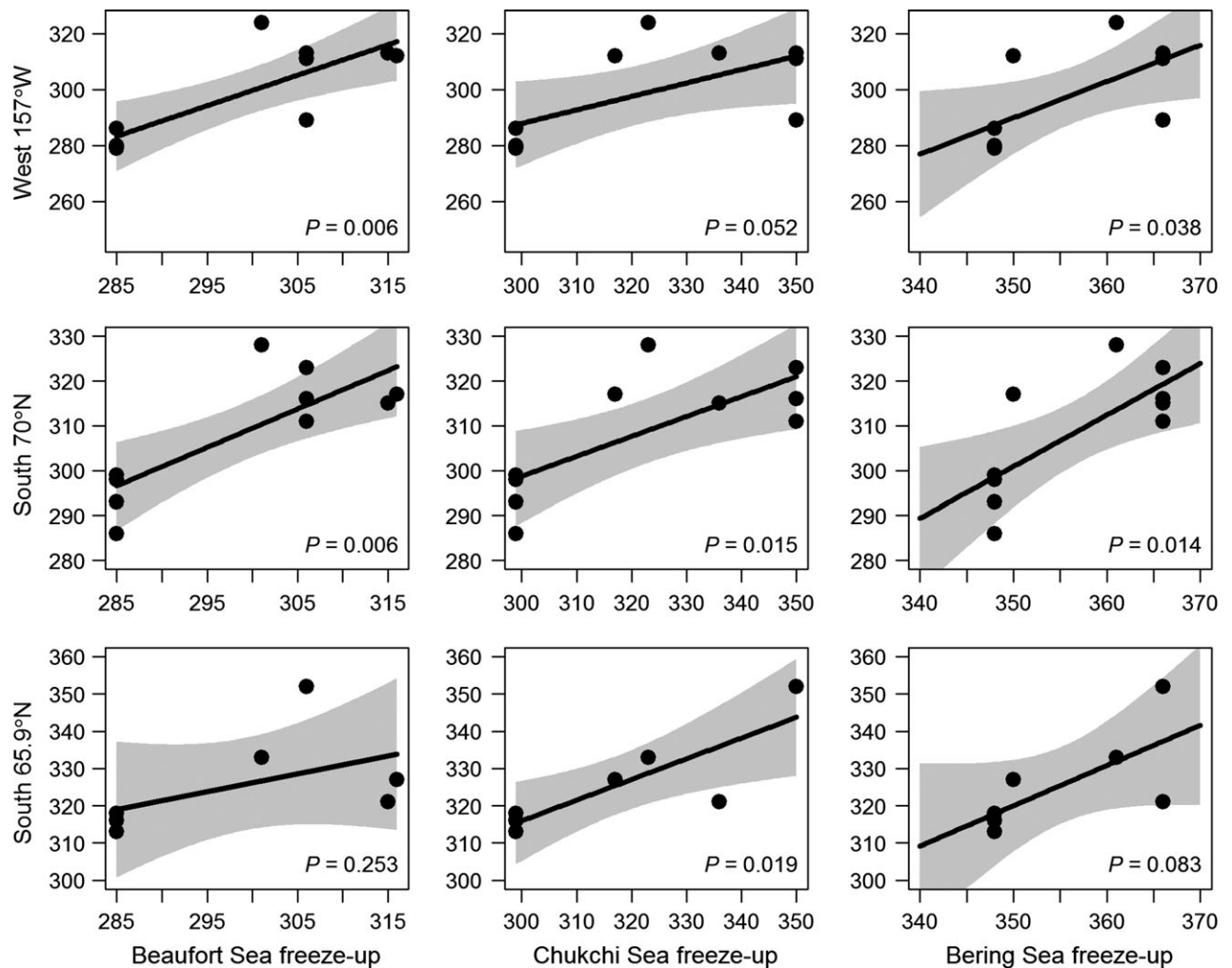
Fig. 3 Linear relationships between Chukchi beluga migration passage day of year (DOY) at each passage boundary compared to freeze-up DOY in the Beaufort Sea (left column), Chukchi Sea (middle column), and Bering Sea (right column). Full statistical details are reported in Table S2.

timing of reproduction, foraging, and other critical behaviors (e.g., Jay *et al.*, 2012; Cherry *et al.*, 2013; Rode *et al.*, 2014; Hamilton *et al.*, 2015).

We used two independent data sources to show consistent trends toward delayed autumn departure for Chukchi belugas from the Beaufort and Chukchi seas. Our acoustic data provided an Eulerian perspective over a shorter time frame that overlapped and extended the 'late' period telemetry data. Our telemetry data offered higher resolution Lagrangian tracks of individuals as they moved across different passage boundaries. There were assumptions associated with each dataset. Passive acoustics relies on belugas vocalizing in close proximity to hydrophones (~5–15 km), and we could not ascertain population identity from vocalizations. However, the Beaufort Sea hydrophone was placed near a Chukchi beluga summer–fall core area (Hauser *et al.*, 2014), and previous work supports our assumption that vocalizations after September would specifically detect Chukchi belugas (Garland *et al.*, 2015a; Richard *et al.*, 2001; Stafford *et al.*, in press, Suydam *et al.*, 2001). Both populations transit near the Bering Strait hydrophone in autumn (Hauser *et al.*, 2014; Citta *et al.*, 2016), in contrast, so we expect both populations were acoustically detected and examined median passage dates accordingly. There were also relatively few years of data to detect changes in migration timing from acoustic data, and all of those data fell within the late period for tagged whales.

For telemetry data, we assumed our limited sample sizes of tagged whales were representative of entire populations and similar between time periods. Recent evidence shows that Chukchi males migrate from the Beaufort Sea later (~1 week) than females (Hauser *et al.*,
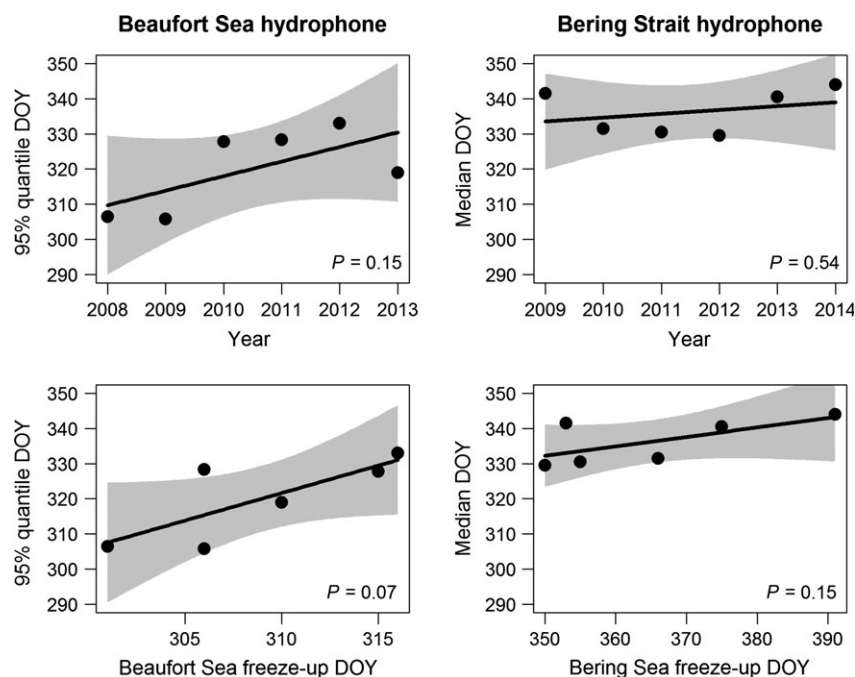
Fig. 4 Linear regressions (and 95% confidence intervals) of the passage day of year (DOY) when belugas were detected at the Beaufort Sea hydrophone from 2008 to 2013 (top left) and at the Bering Strait hydrophone from 2009 to 2014 (top right), and compared with freeze-up timing in the Beaufort Sea (Beaufort Sea hydrophone; bottom left) or Bering Sea (Bering Strait hydrophone; bottom right). We assumed the 95% quantile DOY of beluga vocalizations after September 30 was representative of Chukchi beluga departure from the Beaufort Sea based on the literature (see text). Chukchi and Beaufort belugas overlap in the Bering Strait, so we used median DOY of beluga vocalizations at the Bering Sea hydrophone to consider passage date of both populations. Note that freeze-up in the Bering Sea sometimes did not occur until early the following year, so DOY can be >365.

2014), but we did not examine sex-based differences in migration timing due to small sample size. Nearly equal proportions of Chukchi males and females made up our late period sample, and more males were tagged than females in the early period (Table S1). Thus, if anything, we would expect autumn migration timing of the Chukchi population to have been biased later in the early period due to the greater proportion of males in the early period sample. Migration timing of males and females in the Beaufort population is not significantly different (Hauser *et al.*, 2014), so we do not expect sex-based migration timing would have changed conclusions about changes in Beaufort beluga migration timing. Ultimately our inferential power comes from the combination of these independent data sources despite the specific limitations of each, and we found consistent results across datasets in beluga migration phenology as it relates to regional changes in sea ice freeze-up.

Our analyses of spatial distribution and displacement, passage boundaries, and acoustics all suggest that Chukchi belugas are now remaining in the Pacific Arctic regions for longer in the autumn. Some recent assessments suggest sea ice decline may actually be positive for seasonal migrants as well as some upper

trophic-level marine predators due to ice-related changes in biophysical forcing (Bhatt *et al.*, 2014; Moore & Stabeno, 2015; Moore, 2016). Longer ice-free seasons in combination with increased wind-driven mixing have increased the heat content in upper ocean layers of the Pacific Arctic, likely contributing to enhanced primary and secondary production as well as zooplankton advection (Pickart *et al.*, 2009; Arrigo & Van Dijken, 2015; Wood *et al.*, 2015). Accordingly, body condition of bowhead whales (*Balaena mysticetus*) in the Beaufort Sea improved during 1989–2011 and correlated with sea ice declines (George *et al.*, 2015), fitting predictions for more productive foraging during the recent reduced ice regime (Moore, 2016). Limited time series are available to demonstrate that an increased and extended duration of lower-level productivity is also generating improved foraging opportunities for belugas. One primary prey item, Arctic cod (*Boreogadus saida*), is the dominant and most widespread fish species in recent benthic and pelagic surveys across the Pacific Arctic, in addition to other beluga prey species that appear to be expanding their range into the region (Logerwell *et al.*, 2015). Barrow Canyon and the Beaufort Sea slope are considered summer and autumn 'hotpots' for Chukchi

belugas where oceanographic conditions promote pelagic aggregations of fish, thereby improving foraging opportunities for belugas (e.g., Moore *et al.*, 2000; Stafford *et al.*, 2013; Hauser *et al.*, 2015). Given regional trends toward improved lower-level productivity and prolonged open-water seasons, we expect that foraging opportunities for Chukchi belugas were more extensive and productive in the late than early tagging period.

Our telemetry and acoustic data consistently revealed that autumn migration timing for Chukchi belugas was associated with the onset of freeze-up, particularly in the regions that whales were departing. These results suggest that access to Beaufort and Chukchi sea foraging areas is limited by the annual advance of fast ice, similar to beluga distribution elsewhere (e.g., Heide-Jørgensen *et al.*, 2010). The formation of autumn fast ice in the Chukchi and Beaufort seas is dynamic and rapid, but has been particularly delayed since 2000 due to intensified thermal and wind-driven processes (Frey *et al.*, 2015). Therefore, our results support a conclusion that Chukchi beluga presence north of Bering Strait is temporally constrained by the advance of fast ice and that belugas can respond to variations in the timing of freeze-up.

We found limited evidence that Beaufort beluga westward migration from the Beaufort Sea was similarly influenced by sea ice advance, so other factors may cue migration into the Chukchi Sea for Beaufort belugas. We presume this part of the migration is motivated by predictable foraging opportunities. Maximum and modal depths of diving Beaufort belugas typically target the seafloor in the Chukchi Sea (Hauser *et al.*, 2015), which is characterized by productive benthic invertebrates and Arctic cod prey (Norcross *et al.*, 2013; Grebmeier *et al.*, 2015), except near Herald Canyon where diving targeted mid-water depths and oceanographic properties may establish conditions favorable for pelagic foraging (Pickart *et al.*, 2010; Spall *et al.*, 2014). Beaufort belugas remain north of 70° N in the Herald Canyon region during October before shifting south to the southwestern and southcentral Chukchi Sea in November where the two populations overlap (Hauser *et al.*, 2014). Furthermore, Beaufort belugas may not detect as strong of a sea ice signal in the western portion of the Chukchi Sea relative to the eastern portion used by Chukchi belugas, which is more strongly influenced by Bering Strait advection. While foraging is likely related to Beaufort beluga westward migration from the Beaufort into the Chukchi Sea, additional research is needed to identify factors influencing southward migration. Supplementary data are required to identify other potential factors that may drive migration such as prey availability, sea surface temperature (Bailleul *et al.*, 2012a), other climate indicators of ecosystem productivity related to foraging (Loseto *et al.*, 2015), or simply a more static predictor of heritable migration timing such as day length.

Bering Strait is a constriction point in the fall migration of Pacific Arctic belugas, yet we had the least data for this passage boundary. Bering Strait was the only passage boundary where migration timing of both populations was related to regional freeze-up timing, evidenced by our telemetry data and weakly supported by acoustics. We had a limited sample of tagged Beaufort belugas, but migration south of Bering Strait was later for Beaufort than Chukchi belugas (~2 weeks). Thus, our telemetry results suggested that the autumn advance of sea ice influences timing of exit from the southern Chukchi Sea for both populations. Passive acoustics further supported a conclusion that belugas delayed migration through Bering Strait over time, which was related to the timing of ice formation in the northern Bering Sea, albeit weakly and with unknown population identification. Belugas are typically recorded at the Bering Strait hydrophone in November and early December, and often in pulses separated by multiple days (K. Stafford unpublished data; see Fig. S2). It is unclear whether individuals may linger near the hydrophone location, or whether pulses represent distinct populations. Unlike in the Chukchi Sea, freeze-up timing in the northern Bering Sea has not changed (Laidre *et al.* 2015b). As a result, whales would need to transit the Bering Strait chokepoint before they may necessarily need to exit the Chukchi Sea, explaining the stronger association with Bering Sea freeze-up timing over the Chukchi Sea. Overall, we have the greatest uncertainty in whether there have been phenological changes in migration timing at the Bering Strait, due largely to small sample sizes at this location from both telemetry and acoustic datasets.

Although sea ice freeze-up has been progressively delayed over the satellite record (i.e., since 1979), the trends have been particularly accelerated over the past decade (Frey *et al.*, 2015). Our 'late' period tagging for Beaufort belugas occurred in 2004–2005, before the most dramatic sea ice changes occurred (e.g., 2007 and 2012), but after a transition in Beaufort and Chukchi sea ice regimes commencing around 2002 (Fig. S1; Close *et al.*, 2015; Moore & Stabeno, 2015). The limited relationships found between Beaufort beluga migration timing and regional sea ice freeze-up trends may be due to not having data from tagged whales during the years with largest contrasts in sea ice regimes. Overall the ability to detect climate-related responses is generally limited by our relatively short time series for both populations. Long-term studies and larger sample sizes have greater capacity to detect and attribute biological responses to

changing conditions (Brown *et al.*, 2011; O'Connor *et al.*, 2015), although our datasets were typical of marine biological response studies in many disciplines (Hauser *et al.*, 2016). In any case, continued monitoring of both populations will help elucidate phenological responses by Pacific Arctic beluga populations.

More data are needed to further understand population-specific migration timing, but an important result of our study was that there were non-uniform phenological responses between sympatric beluga whale populations to shifts in regional sea ice freeze-up timing. Understanding variability among populations is particularly relevant to management and planning for the effects of climate change at regional scales (Laidre *et al.*, 2015). Variable responses to climate signals among populations may result from multiple factors such as distinct patterns of utilization, population productivity, life history strategies, or trophic interactions (Post *et al.*, 2009; Gilg *et al.*, 2012), which complicate predictions of species success or failure in the context of transforming ecosystems (Moritz & Agudo, 2013; Post *et al.*, 2013; Rode *et al.*, 2014). Distinct responses by beluga populations to shifting sea ice may reflect plasticity in the face of dynamic Arctic conditions over the last several million years. Indeed, not all neighboring beluga populations within Hudson Bay, Canada, seasonally migrate, possibly because recent sea ice reductions have provided suitable conditions for some to remain over the winter (Bailleul *et al.*, 2012b). Belugas are long-lived (e.g., oldest Beaufort whales observed >60 years; Harwood *et al.*, 2014) with predictable matrilineally derived migrations (Colbeck *et al.*, 2013), so individuals of each Pacific Arctic population have experienced dramatic physical changes within their lifespans. The phenological changes we detected for Chukchi belugas indicate strong adaptive capacity by individuals. In contrast, our results suggest that Beaufort belugas have not strongly responded to the changing environmental stimulus within the decades of our study. Behavioral flexibility among individuals and populations may facilitate adaptive responses by belugas as a species, although it is still hard to anticipate what changing phenologies, or possible non-response, will mean for long-term population persistence. Trends in population abundance are lacking for Chukchi and Beaufort belugas (Laidre *et al.*, 2015), but future research should examine population-scale implications to life histories and demography. For example, measures of body condition, sampled from subsistence-harvested belugas (Suydam, 2009; Harwood *et al.*, 2014), could be compared to changing sea ice conditions (e.g., George *et al.*, 2015).

Shifts in migration timing are not only ecologically meaningful, but also affect many indigenous communities who have relied on belugas for subsistence, cultural, and spiritual resources over millennia. Changes in migration phenology could impact the accessibility and availability of belugas to hunters; however, most harvests of Chukchi and Beaufort belugas in Alaska and western Canada occur in the spring and early summer when we have limited tagging data. Additional studies and data that can further illuminate changes in both spring and autumn migrations will enhance our ability to understand future beluga responses as well as resource security for people who depend on them.

References

Arrigo KR, Van Dijken GL (2015) Continued increases in Arctic Ocean primary production. *Progress in Oceanography*, **136**, 60–70.

Bailleul F, Lesage V, Power M, Doidge DW, Hammill M (2012a) Migration phenology of beluga whales in a changing Arctic. *Climate Research*, **53**, 169–178.

Bailleul F, Lesage V, Power M, Doidge DW, Hammill MO (2012b) Differences in diving and movement patterns of two groups of beluga whales in a changing Arctic environment reveal discrete populations. *Endangered Species Research*, **17**, 27–41.

Barnhart KR, Miller CR, Overeem I, Kay JE (2016) Mapping the future expansion of Arctic open water. *Nature Climate Change*, **6**, 280–285.

Bhatt US, Walker DA, Walsh JE *et al.* (2014) Implications of Arctic sea ice decline for the earth system. *Annual Review of Environment and Resources*, **39**, 57–89.

Börger L, Franconi N, De Michele G *et al.* (2006) Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, **75**, 1393–1405.

Brown CJ, Schoeman DS, Sydeman WJ *et al.* (2011) Quantitative approaches in climate change ecology. *Global Change Biology*, **17**, 3697–3713.

Cavalieri DC, Parkinson CL, Gloersen P, Zwally HJ (1996) *Sea ice Concentrations From Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data, Version 1, 1979–2014*. NASA National Snow and Ice Data Center, Distributed Active Archive Center, Boulder, CO.

Cherry SG, Derocher AE, Thiemann GW, Lunn NJ (2013) Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. *Journal of Animal Ecology*, **82**, 912–921.

Citta JJ, Richard P, Lowry LF *et al.* (2016) Satellite telemetry reveals population specific winter ranges of beluga whales in the Bering Sea. *Marine Mammal Science*. doi: 10.1111/mms.12357.

Close S, Houssais MN, Herbaut C (2015) Regional dependence in the timing of onset of rapid decline in Arctic sea ice concentration. *Journal of Geophysical Research: Oceans*, **120**, 8077–8098.

Colbeck GJ, Duchesne P, Postma LD, Lesage V, Hammill MO, Turgeon J (2013) Groups of related belugas (*Delphinapterus leucas*) travel together during their seasonal migrations in and around Hudson Bay. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122552.

Cresswell KA, Satterthwaite WH, Sword GA (2011) Understanding the evolution of migration through empirical examples. In: *Animal Migration: A Synthesis* (eds Milner-Gulland EJ, Fryxell JM, Sinclair ARE), pp. 7–16. Oxford University Press, New York, NY.

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

Frey KE, Moore GWK, Cooper LW, Grebmeier JM (2015) Divergent patterns of recent sea ice cover across the Bering, Chukchi, and Beaufort seas of the Pacific Arctic Region. *Progress in Oceanography*, **136**, 32–49.

Frost KJ, Lowry LF (1990) Distribution, abundance, and movements of beluga whales, *Delphinapterus leucas*, in coastal waters of western Alaska. In: *Advances in Research on the Beluga Whale, Delphinapterus Leucas* (eds Smith TG, St. Aubin DJ, Geraci JR), pp. 39–57. Canadian Bulletin of Fisheries and Aquatic Sciences 224, Ottawa.

Garland E, Berchok C, Castellote M (2015a) Temporal peaks in beluga whale (Delphinapterus leucas) acoustic detections in the northern Bering, northeastern Chukchi, and western Beaufort Seas: 2010–2011. *Polar Biology*, **38**, 747–754.

Garland EC, Castellote M, Berchok CL (2015b) Beluga whale (*Delphinapterus leucas*) vocalizations and call classification from the eastern Beaufort Sea population. *The Journal of the Acoustical Society of America*, **137**, 3054–3067.

George JC, Druckenmiller ML, Laidre KL, Suydam R, Person B (2015) Bowhead whale body condition and links to summer sea ice and upwelling in the Beaufort Sea. *Progress in Oceanography*, **136**, 250–262.

Gervaise C, Simard Y, Roy N, Kinda B, Ménard N (2012) Shipping noise in whale habitat: characteristics, sources, budget, and impact on belugas in Saguenay–St. Lawrence Marine Park hub. *The Journal of the Acoustical Society of America*, **132**, 76–89.

Gilg O, Kovacs KM, Aars J *et al.* (2012) Climate change and the ecology and evolution of Arctic vertebrates. *Annals of the New York Academy of Sciences*, **1249**, 166–190.

Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and Sub-Arctic seas. *Annual Review of Marine Science*, **4**, 63–78.

Grebmeier JM, Bluhm BA, Cooper LW *et al.* (2015) Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. *Progress in Oceanography*, **136**, 92–114.

Haining R (2003) *Spatial Data Analysis*. Cambridge University Press, Cambridge.

Hamilton CD, Lydersen C, Ims RA, Kovacs KM (2015) Predictions replaced by facts: a keystone species' behavioural responses to declining arctic sea-ice. *Biology Letters*, **11**, 20150803.

Harwood LA, Smith TG (2002) Whales of the Inuvialuit Settlement Region in Canada's western Arctic: an overview and outlook. *Arctic*, **55**, 77–93.

Harwood LA, Kingsley MCS, Smith TG (2014) An emerging pattern of declining growth rates in belugas of the Beaufort Sea: 1989–2008. *Arctic*, **67**, 483–492.

Hauser DDW, Laidre KL, Suydam RS, Richard PR (2014) Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*). *Polar Biology*, **37**, 1171–1183.

Hauser DDW, Laidre KL, Parker-Stetter SL, Horne JK, Suydam RS, Richard PR (2015) Regional diving behavior of Pacific Arctic beluga whales *Delphinapterus leucas* and possible associations with prey. *Marine Ecology Progress Series*, **541**, 245–264.

Hauser DDW, Tobin ED, Feifel KM, Shah V, Pietri DM (2016) Disciplinary reporting affects the interpretation of climate change impacts in global oceans. *Global Change Biology*, **22**, 25–43.

Heide-Jørgensen MP, Laidre KL, Borchers DL, Marques TA, Stern H, Simon M (2010) The effect of sea-ice loss on beluga whales (*Delphinapterus leucas*) in West Greenland. *Polar Research*, **29**, 198–208.

Heide-Jørgensen MP, Laidre KL, Quakenbush LT, Citta JJ (2012) The Northwest Passage opens for bowhead whales. *Biology Letters*, **8**, 270–273.

Huntington H, Suydam RS, Rosenberg DH (2004) Traditional knowledge and satellite tracking as complementary approaches to ecological understanding. *Environmental Conservation*, **31**, 177–180.

Jay CV, Fischbach A, Kochnev AA (2012) Walrus areas of use in the Chukchi Sea during sparse sea ice cover. *Marine Ecology Progress Series*, **468**, 1–13.

Johnson DS, London JM, Lea MA, Durban JW (2008) Continuous-time correlated random walk model for animal telemetry data. *Ecology*, **89**, 1208–1215.

Kovacs KM, Lydersen C, Overland JE, Moore SE (2011) Impacts of changing sea-ice conditions on Arctic marine mammals. *Marine Biodiversity*, **41**, 181–194.

Laidre KL, Stirling I, Lowry LF, Wiig O, Heide-Jørgensen MP, Ferguson SH (2008) Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. *Ecological Applications*, **18**, S97–S125.

Laidre KL, Stern H, Kovacs KM *et al.* (2015) Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology*, **29**, 724–737.

Logerwell EA, Busby M, Carothers C *et al.* (2015) Fish communities across a spectrum of habitats in the western Beaufort Sea and Chukchi Sea. *Progress in Oceanography*, **136**, 115–132.

Loseto LL, Stern GA, Macdonald RW (2015) Distant drivers or local signals: where do mercury trends in western Arctic belugas originate? *Science of the Total Environment*, **509–510**, 226–236.

Maslanik J, Stroeve J, Fowler C, Emery W (2011) Distribution and trends in Arctic sea ice age through spring 2011. *Geophysical Research Letters*, **38**, L13502.

Miller PJO (2006) Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *Journal of Comparative Physiology A*, **192**, 449–459.

Moore SE (2000) Variability in cetacean distribution and habitat selection in the Alaskan arctic, autumn 1982–91. *Arctic*, **53**, 448–460.

Moore SE (2016) Is it 'boom times' for baleen whales in the Pacific Arctic region? *Biology Letters*, **12**, 20160251.

Moore SE, Huntington HP (2008) Arctic marine mammals and climate change: impacts and resilience. *Ecological Applications*, **18**, S157–S165.

Moore SE, Stabeno PJ (2015) Synthesis of Arctic Research (SOAR) in marine ecosystems of the Pacific Arctic. *Progress in Oceanography*, **136**, 1–11.

Moore SE, Demaster DP, Dayton PK (2000) Cetacean habitat selection in the Alaskan Arctic during summer and autumn. *Arctic*, **53**, 432–447.

Moritz C, Agudo R (2013) The future of species under climate change: resilience or decline? *Science*, **341**, 504–508.

Norcross BL, Raborn SW, Holladay BA *et al.* (2013) Northeastern Chukchi Sea demersal fishes and associated environmental characteristics, 2009–2010. *Continental Shelf Research*, **67**, 77–95.

O'Connor MI, Holding JM, Kappel CV *et al.* (2015) Strengthening confidence in climate change impact science. *Global Ecology and Biogeography*, **24**, 64–76.

O'Corry-Crowe GM, Suydam RS, Rosenberg A, Frost KJ, Dizon AE (1997) Phylogeography, population structure and dispersal patterns of beluga whale *Delphinapterus leucas* in the western Nearctic revealed by mitochondrial DNA. *Molecular Ecology*, **6**, 955–970.

Orr JR, Joe R, Evic D (2001) Capturing and handling of white whales (*Delphinapterus leucas*) in the Canadian Arctic for instrumentation and release. *Arctic*, **54**, 299–304.

Pickart RS, Moore GWK, Torres DJ, Fratantoni PS, Goldsmith RA, Yang J (2009) Upwelling on the continental slope of the Alaskan Beaufort Sea: storms, ice, and oceanographic response. *Journal of Geophysical Research*, **114**, 1–17.

Pickart RS, Pratt LJ, Torres DJ *et al.* (2010) Evolution and dynamics of the flow through Herald Canyon in the western Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, **57**, 5–26.

Post E, Brodie J, Hebblewhite M, Anders AD, Maier JAK, Wilmers CC (2009) Global population dynamics and hot spots of response to climate change. *BioScience*, **59**, 489–497.

Post E, Bhatt US, Bitz CM *et al.* (2013) Ecological consequences of sea-ice decline. *Science*, **341**, 519–524.

Richard PR, Orr JR, Martin AR (2001) Summer and autumn movements of belugas of the Eastern Beaufort Sea stock. *Arctic*, **54**, 223–236.

Robinson RA, Crick HQP, Learmonth JA *et al.* (2009) Travelling through a warming world: climate change and migratory species. *Endangered Species Research*, **7**, 87–99.

Rode KD, Regehr EV, Douglas DC, Durner G, Derocher AE, Thiemann GW, Budge SM (2014) Variation in the response of an Arctic top predator experiencing habitat loss: feeding and reproductive ecology of two polar bear populations. *Global Change Biology*, **20**, 76–88.

Rode KD, Wilson RR, Regehr EV, St. Martin M, Douglas DC, Olson J (2015) Increased land use by Chukchi Sea polar bears in relation to changing sea ice conditions. *PLoS ONE*, **10**, e0142213.

Seebacher F, Post E (2015) Climate change impacts on animal migration. *Climate Change Responses*, **2**, 5.

Serreze MC, Stroeve J (2015) Arctic sea ice trends, variability and implications for seasonal ice forecasting. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **373**, 20140159.

Shuter JL, Broderick AC, Agnew DJ, Jonzen N, Godley BJ, Milner-Gulland EJ, Thirgood S (2011) Conservation and management of migratory species. In: *Animal Migrations: A Synthesis* (eds Milner-Gulland EJ, Fryxell JM, Sinclair ARE), pp. 172–206. Oxford University Press, New York, NY.

Sjare BL, Smith TG (1986) The vocal repertoire of white whales, *Delphinapterus leucas*, summering in Cunningham Inlet, Northwest Territories. *Canadian Journal of Zoology*, **64**, 407–415.

Spall MA, Pickart RS, Brugler ET, Moore GWK, Thomas L, Arrigo KR (2014) Role of shelfbreak upwelling in the formation of a massive under-ice bloom in the Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, **105**, 17–29.

Stafford KM, Okkonen SR, Clarke JT (2013) Correlation of a strong Alaska Coastal Current with the presence of beluga whales *Delphinapterus leucas* near Barrow, Alaska. *Marine Ecology Progress Series*, **474**, 287–297.

Stafford KM, Ferguson MC, Hauser DDW *et al.* (in press) Beluga whales in the western Beaufort Sea: current state of knowledge on timing, distribution, habitat use and environmental drivers. *Deep-Sea Research Part II: Topical Studies in Oceanography*.

Stroeve J, Serreze M, Holland M, Kay J, Malanik J, Barrett A (2012) The Arctic's rapidly shrinking sea ice cover: a research synthesis. *Climatic Change*, **110**, 1005–1027.

Suydam R (2009) Age, growth, reproduction, and movements of beluga whales (*Delphinapterus leucas*) from the eastern Chukchi Sea. Ph.D. Dissertation. University of Washington. Seattle, WA. 169 pp.

Suydam RS, Lowry LF, Frost KJ, O'corry-Crowe GM, Pikok DJ (2001) Satellite tracking of eastern Chukchi Sea beluga whales into the Arctic Ocean. *Arctic*, **54**, 237–243.

Wassmann P, Duarte CM, Agusti S, Sejr MK (2011) Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology*, **17**, 1235–1249.

Wood KR, Bond NA, Danielson SL, Overland JE, Salo SA, Stabeno PJ, Whitefield J (2015) A decade of environmental change in the Pacific Arctic region. *Progress in Oceanography*, **136**, 12–31.

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**, 164–168.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Details on 65 Beaufort and Chukchi beluga whales ($n = 38$ and $n = 27$, respectively) satellite-tagged during the early (1993–2002) and late (2004–2012) periods. Longevity refers to the number of days from capture until the last location ($\bar{x}_{Beaufort} = 81.9$ days, $\bar{x}_{Chukchi} = 105.0$ days).

Table S2. Results of linear regressions comparing tagged beluga autumn day of migration past each passage boundary and regional freeze-up day of year.

Figure S1. Linear trends in the Bering Sea, Chukchi Sea, and Beaufort Sea freeze-up day of year (DOY) during 1979–2013 (top row) and separated into periods (bottom row) before belugas were tagged (1979–1992), early period (1993–2002) and late period (2004–2012).

Figure S2. Mean number of hours (± standard error, gray bars) each day of the year (DOY) when beluga vocalizations were detected (top row) and the cumulative distribution of days with beluga vocalizations each year (bottom row), for the Beaufort Sea (left column) and Bering Strait (right column) hydrophones.

Figure S3. Linear relationships between Beaufort beluga migration day of year (DOY) at each passage boundary compared to freeze-up DOY in the Beaufort Sea (left column), Chukchi Sea (middle column), and Bering Sea (right column).