


Indirect effects of sea ice loss on summer-fall habitat and behaviour for sympatric populations of an Arctic marine predator

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Abstract

Aim: Climate change is fundamentally altering habitats, with complex consequences for species across the globe. The Arctic has warmed 2–3 times faster than the global average, and unprecedented sea ice loss can have multiple outcomes for ice-associated marine predators. Our goal was to assess impacts of sea ice loss on population-specific habitat and behaviour of a migratory Arctic cetacean.

Location: Arctic Ocean.

Methods: Using satellite telemetry data collected during summer-fall from sympatric beluga whale (*Delphinapterus leucas*) populations (“Chukchi” and “Beaufort” belugas), we applied generalized estimating equations to evaluate shifts in sea ice habitat associations and diving behaviour during two periods: 1993–2002 (“early”) and 2004–2012 (“late”). We used resource selection functions to assess changes in sea ice selection as well as predict trends in habitat selection and “optimal” habitat, based on satellite-derived sea ice data from 1990 to 2014.

Results: Sea ice cover declined substantially between periods, and Chukchi belugas specifically used significantly lower sea ice concentrations during the late than early period. Use of bathymetric features did not change between periods for either population. Population-specific sea ice selection, predicted habitat and the amount of optimal habitat also generally did not change during 1990–2014. Chukchi belugas tracked during 2007–2012 made significantly more long-duration and deeper dives than those tracked during 1998–2002.

Main conclusions: Taken together, our results suggest bathymetric parameters are consistent predictors of summer-fall beluga habitat rather than selection for specific sea ice conditions during recent sea ice loss. Beluga whales were able to mediate habitat change despite their sea ice associations. However, trends towards prolonged and deeper diving possibly indicate shifting foraging opportunities associated with ecological changes that occur in concert with sea ice loss. Our results highlight that responses by some Arctic marine wildlife can be indirect and variable among populations, which could be included in predictions for the future.

KEYWORDS

Arctic ecology, Beaufort Sea, biotelemetry, Chukchi Sea, climate change, *Delphinapterus leucas*, diving behaviour, generalized estimating equation, marine predator, resource selection

1 | INTRODUCTION

Climate change is fundamentally altering wildlife habitat, leading to complex and variable range shifts across a variety of taxa (Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Schloss, Nunez, & Lawler, 2012). Some species already at geographic extremes, such as the poles, may be particularly impacted, as no place on earth has experienced such profound and unprecedented physical changes as the Arctic (Stroeve et al., 2012). Rapid sea ice loss is expected to have complex ecological implications for Arctic marine ecosystems, yet it is challenging to predict due to limited baselines in this remote region (Post et al., 2013). Endemic Arctic marine mammals (AMMs) are adapted to use sea ice habitat (Laidre, Stern, et al., 2015), and these iconic species already may not have the capacity to respond to habitat shifts or loss (Wilson, Regehr, Rode, & St Martin, 2016). While directly attributable implications of changing sea ice conditions have been reported for ice-obligate species (Hamilton, Lydersen, Ims, & Kovacs, 2015; Rode, Amstrup, & Regehr, 2010), few studies examine the potential indirect effects of ice loss such as shifts in behaviour and movements that may result from altered distribution of resources (e.g., prey, optimal habitat) or novel competitors, diseases and predators (Kovacs, Lydersen, Overland, & Moore, 2011).

Distinctive responses among populations, as well as species, further complicate understanding the ramifications, predictive capacity and management efforts under climate change (Moritz & Agudo, 2013). Although less data-rich than terrestrial and temperate systems, several Arctic marine predators have exemplified variable, and sometimes delayed or positive, responses to climate-related sea ice loss (e.g., Crawford, Quakenbush, & Citta, 2015; George, Druckenmiller, Laidre, Suydam, & Person, 2015; Rode et al., 2014). Population and species-specific responses can result from biological differences (e.g., life history strategies and population productivity), distinct exploitation rates or human impacts and different trophic interactions (Laidre, Stern et al., 2015). For example, sympatric beluga whale (*Delphinapterus leucas*) populations exhibited distinct responses in fall migration timing to significantly delayed sea ice freeze-up in the Chukchi and Beaufort Seas (Hauser, Laidre, Stafford, et al., 2017).

These two populations, the Eastern Chukchi Sea ("Chukchi") and Eastern Beaufort Sea ("Beaufort") beluga whales, are ice-associated, follow maternally driven migration routes tied to annual sea ice retreat and advance, and exhibit site fidelity to separate summer core areas in the western and eastern Beaufort Sea, respectively, where they forage in both benthic and pelagic habitats (Hauser et al., 2015; Hauser, Laidre, Stern, et al., 2017; Hauser, Laidre, Suydam, & Richard, 2014; Moore, DeMaster, & Dayton, 2000; O'Corry-Crowe et al., 2016). The loss of Arctic sea ice cover has been particularly pronounced in this Beaufort and Chukchi Sea region (Walsh, Fetterer, Scott Stewart, &

Chapman, 2017), where sea ice extent has been characterized by "breakpoint" decreases in summer-fall extent between the 1990s and 2000s (Close, Houssais, & Herbaut, 2015). Recent expansions of open water also affect regional wind-forcing, hydrography, upwelling and productivity (Pickart et al., 2013; Wood et al., 2015), which in turn presumably indirectly affects beluga foraging opportunities (Stafford, Citta, Okkonen, & Suydam, 2016).

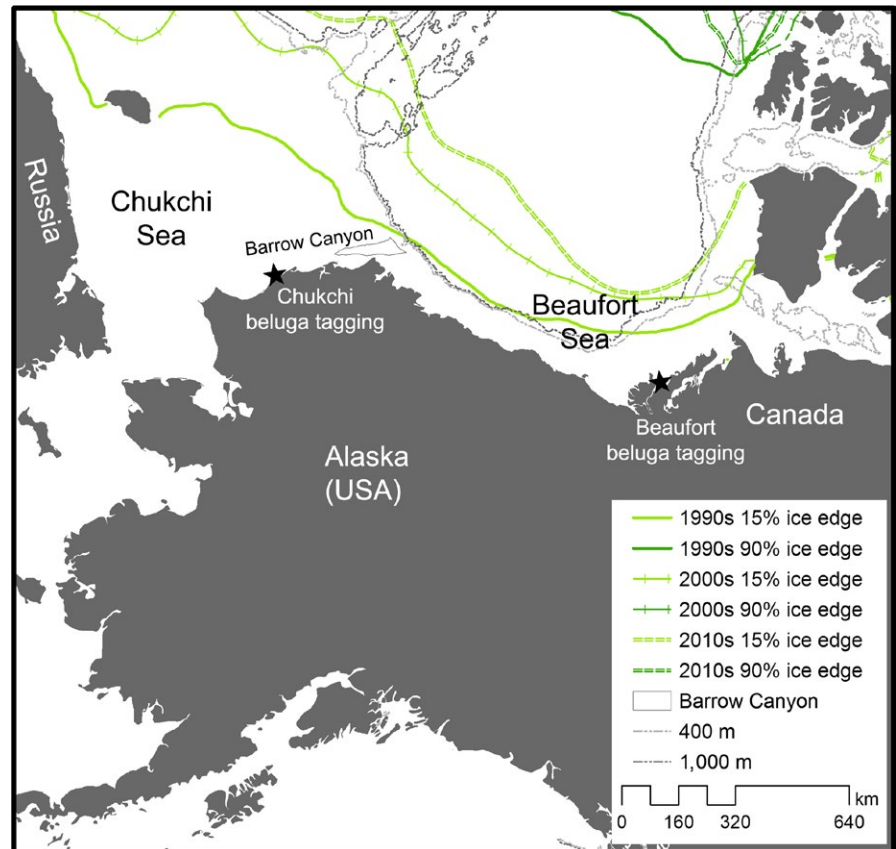
Thus, these sympatric populations must balance strong seasonal site fidelity against the shifting sea ice habitat in which they forage. We capitalized on unique long-term biotelemetry datasets on Chukchi and Beaufort beluga whales to examine responses to dynamic sea ice changes set within the context of stationary bathymetric characteristics, both of which are strong predictors of summer-fall beluga habitat (Hauser, Laidre, Stern et al., 2017). Our objectives focused on contrasting population-specific July–October sea ice associations, habitat selection and diving behaviour between "early" and "late" periods when belugas were tagged (1993–2002 and 2004–2012, respectively). We hypothesized that belugas would use lower sea ice concentrations in recent years due to sea ice retreat within the Chukchi and Beaufort Seas, whereas consistent use of bathymetric features would reflect site fidelity to summer-fall foraging habitat. We tested for changes in the sea ice and bathymetric habitat used by belugas between periods using generalized estimating equations (GEEs). However, a shift in sea ice habitat use between periods would not necessarily mean belugas changed distribution, so we next applied univariate and multivariate resource selection functions to examine how sea ice habitat was used relative to availability across time periods. We used univariate models to specifically test differences in selection of sea ice variables between periods while applying multivariate habitat selection models to quantify if shifts occurred in predicted use during 1990–2014. Multivariate habitat selection models were also used to identify any trends in the amount of predicted "optimal" habitat, 1990–2014. Finally, we presumed changes in diving behaviour could be indirectly related to shifts in foraging opportunities that may occur in association with sea ice loss between periods, and we used GEEs to test changes in a number of diving metrics that are representative of foraging behaviour between periods.

2 | METHODS

2.1 | Beluga satellite telemetry location and diving data

We used satellite telemetry data collected from 65 Beaufort and Chukchi beluga whales tagged in late June–July in the Mackenzie River Estuary from 1993 to 2005 and in north-west Alaska from 1998 to 2012, respectively (Figure 1, Table S1) (Richard, Orr, & Martin,

FIGURE 1 Study area in the Chukchi and Beaufort Seas, including approximate tagging locations (stars) for Chukchi and Beaufort beluga whale populations, bathymetry and mean 15% and 90% ice edge locations during September 1990–1999, 2000–2009 and 2010–2014. Sea ice edges were extracted from mean sea ice concentration grids calculated from the September sea ice concentration in each year (Cavalieri et al., 1996, updated yearly) [Colour figure can be viewed at wileyonlinelibrary.com]



2001; Suydam, Lowry, Frost, O'Corry-Crowe, & Pikok, 2001). We focused analyses on July–October when the most data were available, using a standardized daily location along the track of each whale (Hauser, Laidre, Stern et al., 2017). We compared pooled years when tagging occurred to consider changes in habitat and behaviour, selecting specific periods that correspond to contrasting sea ice conditions and shifts in the Beaufort–Chukchi ecosystem (Close et al., 2015; Hauser, Laidre, Stafford et al., 2017; Moore & Staben, 2015): an “early” period (1993–2002) and “late” period (2004–2012).

All but one tag used for the Chukchi population also provided diving information (Table S1), summarized over four 6-hr periods each day. Similar dive data comparable between periods were not collected for the Beaufort population. The tags on Chukchi belugas collected three types of dive data summarized as histograms for each 6-hr period: the number of dives to pre-defined depths, proportional time within each depth and number of dives to pre-defined duration bins (described in Hauser et al., 2015). We rescaled these data to estimate several daily diving metrics, including dive rates (total dives/d, dives/d to <10 m, dives/d < 1 min, dives/d > 20 min), proportion of time <10 m and mean dive depth. We ascribed water depths to each daily location (see Hauser et al., 2015) to additionally create a binary predictor of whether the maximum daily dive depth reached the seafloor as an indicator of proximity to benthic habitat (i.e., “benthic-oriented diving”). Diving data can be used to infer behaviour at depth, and we assumed that daily dive depth, rates (daily and >20 min) and benthic-oriented diving were related to foraging (Hauser et al., 2015). In contrast, we assumed short-duration (<1 min) dives as well as dive rates

and proportional time near the surface (<10 m) was representative of surface-based recovery, travel or resting.

2.2 | Changes in habitat associations and habitat selection

We matched a set of four sea ice characteristics to each beluga daily location based on daily sea ice concentration values estimated from satellite passive microwave data (SSM/I), available at a nominal grid resolution of 25 km (Cavalieri, Parkinson, Gloersen, & Zwally, 1996; updated yearly). Each sea ice variable was previously identified as a contributing factor to beluga summer–fall habitat selection (Hauser, Laidre, Stern et al., 2017). We extracted the daily sea ice concentration at each whale location as well as the nearest distance to the daily 15% sea ice edge and to dense pack ice (i.e., 90% concentration). For each day, we also created a binary variable identifying whether whales were located within open water or among pack ice (>15% concentration). We assigned depth and slope values to each daily location based on the ETOPO1 global relief map (Amante & Eakins, 2009), as described by Hauser, Laidre, Stern et al. (2017).

We assessed changes in ice and bathymetric habitat used by whales between early and late periods using nested GEEs, which are extensions of generalized linear models that facilitate regressions of longitudinal data (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The assumption of independent model errors is replaced by specifying a correlation structure, and GEEs have been successfully applied to telemetry and distribution data including habitat analyses for marine

mammals (e.g., Bailey, Corkrey, Cheney, & Thompson, 2013; Russell et al., 2015). GEEs use sandwich-based estimates of variance so the uncertainty around parameter estimates is robust to the presence of serial autocorrelation within individuals while not explicitly modelling the correlation, so are commonly used when the population-averaged response (marginal mean) is of primary interest (Hardin & Hilbe, 2013). Thus, the mean response reflects only the covariates and not the random effects (Zuur et al., 2009). We built Gaussian-nested GEEs using the R package “geepack” (Højsgaard, Halekoh, & Yan, 2006) to model population-specific beluga sea ice and bathymetric associations (i.e., mean concentration used, distance to 15% ice edge, distance to 90% ice edge, depth and slope). We used the binomial distribution to model the probability of being located in pack ice. In all cases, we applied an autoregressive (“AR1”) correlation structure to take into account the temporal dependence among observations, which were clustered for each individual whale. Our models included month and sex as factors to account for monthly movements and sexual segregation (Hauser et al., 2014; Loseto, Richard, Stern, Orr, & Ferguson, 2006) and also measured the effect of period (early, late), using Wald tests for model selection.

We used two approaches to examine possible changes in population-specific summer-fall habitat selection over time. First, we compared sea ice selection between periods as the sea ice habitat used by whales (concentration, distances to 15% and 90% ice) relative to availability by applying a case-control univariate conditional logistic regression approach, which has been successfully used to test shifts in polar bear (*Ursus maritimus*) sea ice selection (Laidre, Born et al., 2015). These univariate between-period comparisons specifically focused on the sea ice variables that have changed between periods rather than the stationary bathymetric variables, testing whether each sea ice parameter used by belugas in the early period was different than that used in the late period given changes in availability. We used the “clogit” function in the “survival” package in R (Therneau, 2015), establishing habitat availability for each observed beluga location based on a set of 25 random locations within a circular buffer representing plausible daily movement trajectories (see Hauser, Laidre, Stern et al., 2017).

Applying monthly sex- and population-specific habitat selection models developed by Hauser, Laidre, Stern et al. (2017), we also measured shifts in the spatial distribution and amount of habitat selected each year, 1990–2014. These multivariate habitat selection models always included some combination of sea ice and bathymetric predictor variables (as determined by final model selection in Hauser, Laidre, Stern et al., 2017), and were used to produce monthly male and female maps of relative probability of use for each year. Specifically, we mapped the spatial distribution of predicted habitat and identified “optimal habitat” as grids with $\geq 75\%$ predicted probability of use. We estimated 1990–2014 trends in the amount of monthly optimal habitat using least-squares regression.

2.3 | Changes in Chukchi beluga diving behaviour

We evaluated shifts in daily diving behaviour of the Chukchi population between periods using GEEs, for which we again specified an

autoregressive correlation structure on clustered observations of each individual whale. We included sex, month and period as predictors of each daily diving metric as well as an interaction factor for month \times period, using Wald tests for model selection. We modelled each dive rate response with Poisson errors while proportional time at depth and mean dive depth were log-transformed and modelled using the Gaussian distribution. We estimated the probability that maximum dive depths coincided with the seafloor (i.e., benthic-oriented diving) using the binomial distribution.

3 | RESULTS

3.1 | Changes in sea ice habitat associations and selection

Month and sex were consistent predictors of habitat associations for both beluga populations (Table 1, Figure S1), as expected. However, period was a significant factor for sea ice habitat use by Chukchi belugas but not by Beaufort belugas, indicating that sea ice habitat used by Chukchi whales significantly changed between the early and late periods. Specifically, significantly heavier ice and closer proximity to the 90% ice edge were used by Chukchi whales tracked in 1998–2002 (early period) compared to those in 2007–2012 (late period). Chukchi whales tagged during the early period were also significantly more likely to be located in pack ice ($>15\%$ concentration) than those tagged in the late period. Bathymetric habitat used did not change for either population between periods. Period was not significant in exploratory models during model selection, so period was ultimately not included in the final population models as a predictor of bathymetric habitat.

Despite changes in the ice habitat used by Chukchi belugas between periods, there were few significant changes in the sea ice habitat selected relative to what was available by either population in the early versus late period (Table S2). There were also few cases where the spatial distribution of predicted habitat shifted during 1990–2014 (Figure S2). The most striking changes in the predicted probability of use occurred in October for Chukchi males and females, suggesting a prolonged occupation of the continental slope or near Barrow Canyon in the Beaufort Sea in the 2000s compared to use of the Chukchi Sea in the 1990s. The amount of optimal habitat, 1990–2014, was invariant for both populations in all months except one (Table 2), although the majority (69%) of the 13 monthly trends were negative.

3.2 | Changes in behaviour

A suite of diving metrics indicated that Chukchi belugas tagged during 2007–2012 (late period) spent more time at deeper depths than those tagged during 1998–2002 (early period). Less time was spent near the surface in the late period, evidenced by fewer short-duration and shallow dives (i.e., dives/day <10 m or <1 min, percentage of time <10 m) and a lower overall daily dive rate (Table 3). There were more long-duration (>20 min) dives corresponding with deeper mean dive depths, and maximum dive depths were more likely to reach the seafloor in the late period (Table 3, Figure 2). Month was also a significant

TABLE 1 Summary statistics and factors affecting habitat used by Chukchi and Beaufort populations of beluga whales revealed using generalized estimating equations

	Chukchi belugas			Beaufort belugas		
	<i>Mean ± SE habitat early, late</i>			<i>Mean ± SE habitat early, late</i>		
	df	χ^2	<i>p</i>	df	χ^2	<i>p</i>
<i>Probability of being located in sea ice (>15%)</i>						
Month	3	7.6	0.054			
Sex	1	6.6	0.014	1	6.7	0.010
Period	1	17.4	<0.001			
<i>Sea ice concentration (%)</i>						
Month	3	9.4	0.025	4	9.8	0.043
Sex	1	14.7	<0.001	1	5.6	0.019
Period	1	27.9	<0.001			
<i>Proximity to 15% ice edge (km)</i>						
Month	3	59.3	<0.001	3	40.2	<0.001
Sex				1	12.6	<0.001
<i>Proximity to 90% ice edge (km)</i>						
Month	3	12.8	0.005	3	11.2	0.011
Sex	1	2.6	0.108	1	6.0	0.014
Period	1	57.6	<0.001			
<i>Depth (m)</i>						
Month	3	82.6	<0.001	3	17.0	<0.001
Sex	1	6.1	0.014	1	4.0	0.047
<i>Slope (%)</i>						
Month	3	76.6	<0.001	3	26.0	<0.001
Sex				1	4.9	0.027

^aMeasure of the proportion of locations in ice during the early and late periods.

Bolded *p*-values indicate factors are significant at $p < 0.05$. Blank factors were not included in final model selection. Mean (\pm SE) habitat used by belugas tagged in the early (1993–2002) and late (2004–2012) periods is indicated in italics for each variable.

TABLE 2 Trends in the amount of predicted optimal habitat for Chukchi and Beaufort beluga whales in July to October, 1990–2014

Month	Chukchi male (km ² /y)	Chukchi female (km ² /y)	Beaufort male (km ² /y)	Beaufort female (km ² /y)
July	−102.9	+17.8	−19.7	−197.1
August	+16.3	−103.4	−25.5	−305.8
September	+34.1	−240.9	+10.9	
October	−242.3	−138.9		

Bolded values indicate significance at $p < 0.05$. One outlier for Beaufort males in September 2014 (59,375 km²) was excluded from the trend analysis, and months with poor predictive capacity for Beaufort belugas are excluded (see Hauser, Laidre, Stern et al., 2017).

factor for nearly all diving metrics, as would be expected due to differences in water depths used by belugas each month (Hauser et al., 2015). Thus, period or an interaction between month and period was a significant predictor of all but one diving metric (i.e., number of

dives/d < 10 m). Patterns for deeper, longer dives in the late period were consistent each month, July–October, but the strongest contrasts were in July and October (Figure 2). We found limited evidence of sex-based differences in diving behaviour.

TABLE 3 Summary statistics and factors affecting a suite of daily diving metrics for Chukchi beluga whales based on generalized estimating equations (GEEs)

	Mean (SE)		GEE inference		
	Early	Late	df	χ^2	p
<i>Daily dive rate (dives/d)</i>	12.8 (0.2)	10.6 (0.2)			
Month			3	1.0	0.802
Period			1	3.8	0.050
Period:Month			3	15.0	0.002
<i>Dives/d < 10 m</i>	8.3 (0.2)	6.5 (0.2)			
Month			3	26.2	<0.001
<i>Dives/d < 1 min</i>	6.3 (0.2)	3.9 (0.2)			
Month			3	15.8	0.001
Period			1	5.6	0.018
<i>Dives/d > 20 min</i>	0.9 (0.03)	2.8 (0.07)			
Period			1	75.9	<0.001
<i>Percentage of time <10 m</i>	56.6 (1.0)	49.1 (1.1)			
Month			3	10.3	0.016
Sex			1	7.9	0.005
Period			1	9.7	0.002
Period:Month			3	10.0	0.018
<i>Daily dive depth (m)</i>	49.3 (1.7)	64.0 (1.9)			
Month			3	153.0	<0.001
Period			1	30.1	<0.001
Period:Month			3	80.4	<0.001
<i>Probability maximum dive depth reaches the seafloor</i>	0.455	0.495 ^a			
Month			3	27.3	<0.001
Sex			1	10.3	0.001
Period			1	0.4	0.532
Period:Month			3	16.9	<0.001

^aMeasure of the proportion reaching the seafloor in the early and late periods.

Bolded *p*-values indicate factors are significant at *p* < 0.05. Unlisted factors were not included in final GEE model selection.

4 | DISCUSSION

Arctic marine ecosystems are rapidly transforming in the face of climate change, yet measures of biological responses to sea ice loss are multifaceted and have been particularly limited for most upper trophic-level species (Post et al., 2013; Wassmann, Duarte, Agusti, & Sejr, 2011). We present one of the first comprehensive analyses of the indirect effects of changing sea ice regimes on population-specific habitat use and behaviour of an Arctic cetacean. Our results supplement a growing

assemblage of indicators suggesting the ecosystem of the Beaufort and Chukchi Seas is in flux, with several emergent properties since 2004 (Moore & Stabeno, 2015). One of our most striking results was that both beluga populations have generally not changed their summer-fall habitat selection despite long-term and persistent reductions in sea ice cover that have changed the sea ice attributes available to at least Chukchi belugas. Sea ice cover is not the only determinant of summer-fall beluga habitat selection (Hauser, Laidre, Stern et al., 2017), and our results confirm that sea ice concentrations do not particularly matter to beluga summer distribution. Instead, we found that use of bathymetric habitat predictors did not change between periods, which we suggest indicates that summer distribution may be more governed by site fidelity to particular bathymetric features that promote foraging. Beaufort belugas generally used lower sea ice concentrations than Chukchi belugas, which is presumably why declines in sea ice cover (i.e., between tagging periods) were reflected in the habitat used by Chukchi belugas but not for Beaufort belugas. Especially for Chukchi whales, changes in habitat associations between periods are likely a consequence of sea ice retreat from preferred summer habitat, and driven by an affiliation with bathymetric habitat features, rather than a change in distribution. This retreat was most dramatic in July and August for Chukchi belugas when they are particularly predictable in their site fidelity (O'Corry-Crowe et al., 2016), further supported by recent results that home ranges were relatively similar between periods (Hauser, 2016). While neither population generally changed habitat selection between periods, Chukchi belugas have shifted fall migration later with delayed freeze-up timing compared to Beaufort belugas that have not changed fall migration timing (Hauser, Laidre, Stafford et al., 2017). Our results suggest this may be related to the weaker seasonal association with sea ice for Beaufort belugas, particularly in the fall when they move into the Chukchi Sea (where freeze-up occurs later) ahead of Chukchi belugas.

We also found limited evidence of shifts in optimal habitat or probability of use for either population during 1990–2014, further suggesting that sea ice cover has limited effect on beluga habitat selection. For Chukchi belugas, we predicted the highest probability of use shifted eastwards in October during the 2000s, indicating that both males and females would depart the Beaufort Sea later and supporting recent analyses that fall migration out of the Beaufort Sea is positively correlated with delayed Beaufort Sea freeze-up timing (Hauser, Laidre, Stafford et al., 2017). Chukchi beluga migration occurred >1 month later during the late period as freeze-up was also delayed. Combining results from both studies implies that the role of advancing sea ice in the fall may be to limit access to preferred habitat where Chukchi belugas experience productive foraging.

The results of our diving behaviour analyses indicate that sea ice may indirectly impact foraging opportunities during summer-fall for Chukchi belugas, consistently showing that Chukchi belugas spent more time at deeper depths during 2007–2012 than 1998–2002. This shift occurred in all months (July–October), indicative of changing foraging opportunities occurring in concert with sea ice-associated ecosystem changes. Deeper and longer dives could result if prey were more dispersed or deeper, forcing whales to expend more energy searching for prey. Alternatively, there could be more extensive and productive

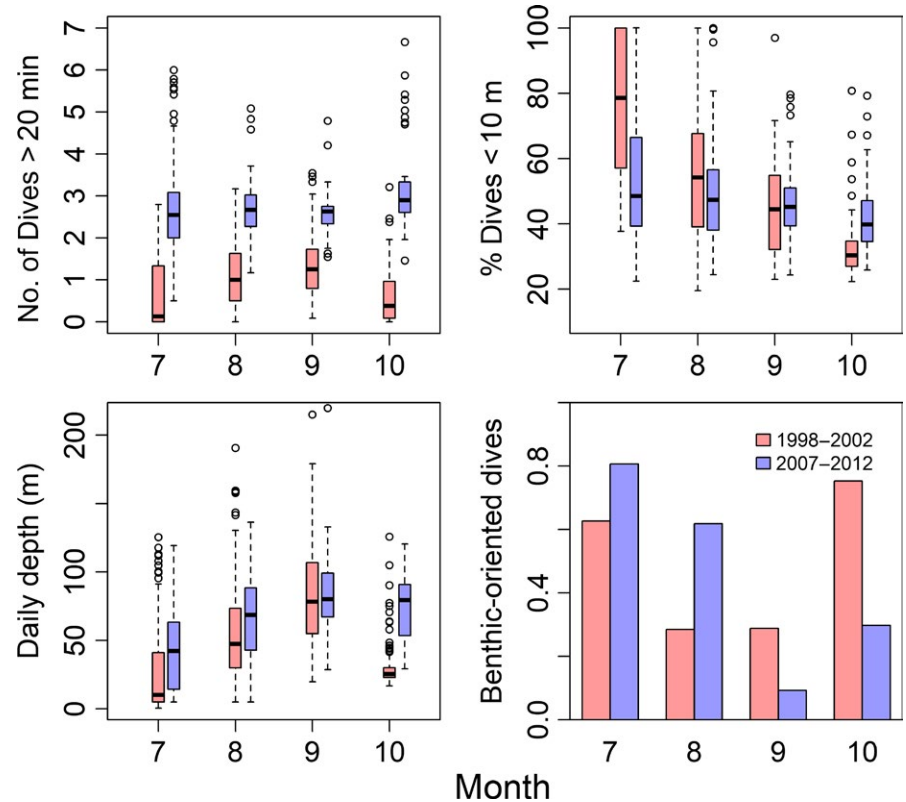


FIGURE 2 Monthly differences in mean number of long-duration dives per day, percentage of time in shallow depths per day, mean daily dive depth and benthic-oriented diving (i.e., the proportion of maximum daily dive depth measures that reached the seafloor) between the early period (1998–2002) and late period (2007–2012) for Chukchi beluga whales [Colour figure can be viewed at wileyonlinelibrary.com]

foraging opportunities in recent years. As the summer melt season has lengthened, increased solar radiation in the upper ocean combined with more storms and wind-forcing has enhanced the creation of hydrographic fronts as well as upwelling of nutrient-rich Atlantic Water onto the Beaufort Sea continental slope and shelves to fuel primary as well as secondary production (Brugler et al., 2014; Pickart et al., 2013; Wood et al., 2015). Recent changes in both upwelling and advection processes enhance water-column secondary production that presumably concentrate pelagic prey such as Arctic cod (*Boreogadus saida*) (Moore & Stabeno, 2015) that are likely targeted by Chukchi belugas in the Alaska Beaufort Sea (Hauser et al., 2015; Stafford, Okkonen, & Clarke, 2013). As a result, diminished ice cover may be improving the extent and concentration of foraging opportunities for belugas, possibly explaining why Chukchi belugas spent more time at depth in the later period. Thus, we hypothesize that changing oceanographic properties, related to reduced ice cover, either create more foraging opportunities, a deeper prey base, or a combination of the two that have contributed to deeper and longer summer-fall dives in recent years for Chukchi belugas.

The implications of deeper, prolonged diving in recent years for the Chukchi population are unclear. On the one hand, changes in diving behaviour could result from improved foraging opportunities that can translate to healthier body condition, similar to bowhead whales (*Balaena mysticetus*) in the region (George et al., 2015). Belugas feed at higher trophic levels than bowheads, yet may be flexible in their response to similarly improved feeding opportunities. Alternatively, increased diving effort is energetically costly for individuals. Chukchi beluga whales, especially juveniles, may already be pushing their physiological limits (Noren & Suydam, 2016), so understanding the

impacts of deeper, longer dives is complicated and warrants additional research.

Our results also underscore the importance of examining population-specific responses to climate change by highlighting differences in the sea ice habitat used by Chukchi and Beaufort belugas. Many of the same regions are used by the two populations during summer-fall but at different times (Hauser et al., 2014), which impacted the ice habitat they encountered (present study) and their access to foraging habitat (Hauser, Laidre, Stafford et al., 2017). Understanding variability between and among populations of Arctic marine mammals is particularly relevant to managing populations experiencing variable effects of climate change at regional scales (Laidre, Stern et al., 2015). This fits with a broader emerging pattern of distinct responses to climate forcing among subpopulations (Moritz & Agudo, 2013), which, in this case, complicates predictions of how belugas may fare in a changing Arctic. Although Beaufort belugas seem to be maintaining a stable or increasing population (Harwood & Kingsley, 2013), other recent evidence suggests decreasing growth rates and body condition (Harwood et al., 2015). Additional effort for long-term monitoring of these and other beluga populations in concert with biophysical indicators of regional ecosystem trends will continue to elucidate population-scale implications of observed and projected sea ice declines.

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DATA ACCESSIBILITY

Sea ice data are available online at <https://doi.org/10.5067/8gq8lzqvl0vl>. The telemetry datasets supporting this article were obtained under an agreement of specific use. Chukchi beluga data are available from the North Slope Borough, and Beaufort beluga data are available from Fisheries and Oceans Canada.

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BIOSKETCH

Donna Hauser is a marine ecologist whose research is broadly centred on understanding the ecological implications of environmental change at high latitudes. Her research focuses on the distribution, movements, habitat use and behaviour of marine predators across multiple spatial and temporal scales. This study expands the Arctic marine mammal and sea ice research by Laidre and Stern and the long-term collaborative efforts to track beluga whales in the Beaufort and Chukchi Seas by Suydam and Richard. Much information about Dr. Hauser's research can be found at <https://donnahauser.wordpress.com/> and the Laidre Lab at <https://staff.washington.edu/klaidre/>.

Author contributions: D.H. and K.L. designed the analysis; D.H. and H.S. analysed the data; R.S. and P.R. led data collection and field logistics; D.H. led the writing; and all authors contributed ideas and to writing of the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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