ARCTIC
VOL. 73, NO. 3 (SEPTEMBER 2020) P. 278–291
https://doi.org/10.14430/arctic70865

Use of the Alaskan Beaufort Sea by Bowhead Whales (*Balaena mysticetus*) Tagged with Satellite Transmitters, 2006–18

Justin Olnes,[1,2] John J. Citta,[1] Lori T. Quakenbush,[1] John C. George,[3] Lois A. Harwood,[4] Ellen V. Lea[5] and Mads Peter Heide-Jørgensen[6]

(*Received 7 November 2019; accepted in revised form 20 April 2020*)

ABSTRACT. We used satellite telemetry to examine bowhead whale movement behavior, residence times, and dive behavior in the Alaskan Beaufort Sea, 2006–18. We explored the timing and duration of use of three subregions (western, central, eastern) within the Alaskan Beaufort Sea and applied a two-state switching state-space model to infer bowhead whale behavior state as either transiting or lingering. Transiting whales made direct movements whereas lingering whales changed direction frequently and were presumably feeding. In spring, whales migrated across the Alaskan Beaufort Sea in 7.17 ± 0.41 days, primarily off the continental shelf over deep water. During the autumn migration, whales spent over twice as much time crossing the Alaskan Beaufort Sea than in spring, averaging 18.66 ± 2.30 days, spending 10.05 ± 1.22 days in the western subregion near Point Barrow. Most whales remained on the shelf during the autumn migration and frequently dove to the seafloor, where they spent 45% of their time regardless of behavioral state. Consistent dive behavior in autumn suggests that the whales were looking for food while migrating, and the identification of lingering locations likely reflects feeding. The lack of lingering locations in the eastern and central subregions suggests that prey densities are rarely sufficient to warrant whales pausing their migration for multiple days, unlike in the western subregion near Point Barrow, where bowhead whales regularly lingered for long periods of time.

Key words: bowhead whale; Alaska; Beaufort Sea; satellite telemetry; dive behavior; feeding; Western Arctic; migration

RÉSUMÉ. À l'aide de la télémétrie satellitaire, nous avons examiné les comportements de déplacement des baleines boréales, leurs temps de séjour et leurs comportements de plongée dans les eaux alaskiennes de la mer de Beaufort entre 2006 et 2018. Nous avons exploré le moment et la durée d'utilisation de trois sous-régions (ouest, centre et est) des eaux alaskiennes de la mer de Beaufort et appliqué un modèle à changement binaire espace-état afin de déduire l'état du comportement des baleines boréales comme étant soit en mode transit, soit en mode flânerie. Les baleines en mode transit se déplaçaient de manière directe, tandis que celles en mode flânerie changeaient souvent de direction et étaient probablement en train de se nourrir. Au printemps, les baleines migraient dans les eaux alaskiennes de la mer de Beaufort en 7,17 ± 0,41 jours, principalement au large du plateau continental, dans les profondeurs. Durant la migration automnale, les baleines passaient plus de deux fois plus de temps à traverser les eaux alaskiennes de la mer de Beaufort qu'au printemps, en moyenne 18,66 ± 2,30 jours, passant 10,05 ± 1,22 jours dans la sous-région de l'ouest, près de Point Barrow. Pendant la migration automnale, la plupart des baleines restaient dans le plateau continental et plongeaient souvent jusqu'au plancher océanique, où elles passaient 45 % de leur temps, peu importe leur état de comportement. À l'automne, le comportement de plongée régulier suggère que les baleines étaient à la recherche de nourriture pendant leur migration, et les lieux où elles flânaient étaient vraisemblablement indicateurs d'un mode d'alimentation. L'absence de lieux de flânerie dans les sous-régions de l'est et du centre suggère que la densité des proies est rarement suffisante pour que les baleines justifient d'interrompre leur migration pendant plusieurs jours, contrairement à la sous-région de l'ouest, près de Point Barrow, où les baleines boréales flânaient régulièrement pendant de longues périodes.

Mots clés : baleine boréale; Alaska; mer de Beaufort; télémétrie satellitaire; comportement de plongée; alimentation; Arctique de l'Ouest; migration

Traduit pour la revue *Arctic* par Nicole Giguère.

[1] Alaska Department of Fish and Game, 1300 College Road, Fairbanks, Alaska 99701, USA
[2] Corresponding author: justin.olnes@alaska.gov
[3] Division of Wildlife Management, North Slope Borough, PO Box 69, Utqiaġvik, Alaska 99723, USA
[4] Department of Fisheries and Oceans Canada, 301-5204 50th Avenue, Yellowknife, Northwest Territories X1A 1E2, Canada
[5] Department of Fisheries and Oceans Canada, PO Box 1871, Inuvik, Northwest Territories X0E 0T0, Canada
[6] Greenland Institute of Natural Resources, Strandgade 91, 2, DK-1401 Copenhagen, Denmark

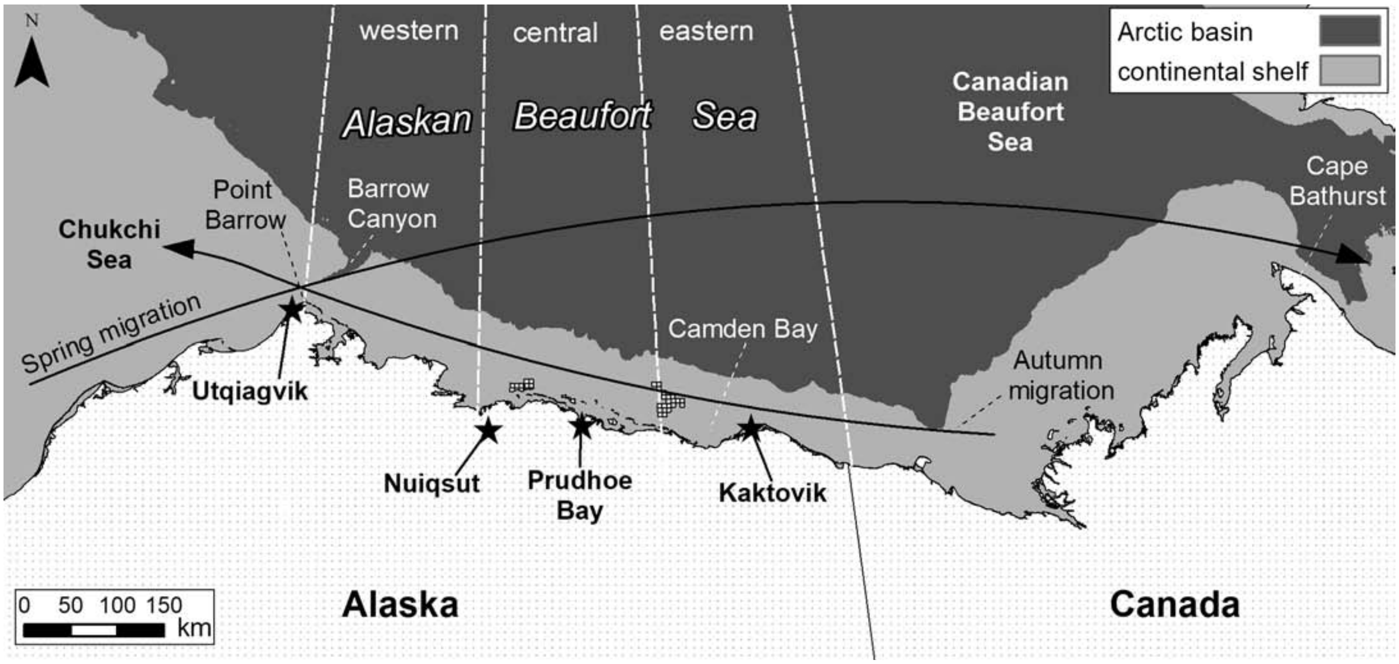

FIG. 1. Map of the Alaskan Beaufort Sea divided into three equal subregions. Solid black lines with arrows show generalized spring and autumn migration routes for the Bering-Chukchi-Beaufort stock of bowhead whales. White squares on the continental shelf are oil and gas leased areas. Continental shelf waters are defined as waters less than 200 m deep.

INTRODUCTION

Bowhead whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort (BCB) stock, also known as the Western Arctic stock, make seasonal migrations between wintering grounds in the Bering Sea and primary summer feeding grounds in the Canadian Beaufort Sea (Moore and Reeves, 1993; Citta et al., 2012, 2015; Harwood et al., 2017). In doing so, bowhead whales typically migrate through the Alaskan Beaufort Sea twice per year, eastward in spring (April–May) and westward in autumn (August–November) (Fig. 1). The Alaskan Beaufort Sea is an important whaling ground for three Alaskan Native communities (Stoker and Krupnik, 1993), and many entities have long-standing concerns that oil and gas exploration and extraction activities may negatively affect bowhead whales and whale hunting success by the communities that depend on them for subsistence (Braund and Kruse, 2009; Reeves et al., 2014). Of primary concern to Native whalers is that these activities may deflect bowhead whales away from important feeding areas and farther offshore where they cannot be harvested (Natural Resource Council, 2003). A recent study, however, suggested that bowhead whales remain in areas of seismic operations and other activities if they are feeding, but alter their surfacing and diving behavior in response to disturbance (Robertson et al., 2016). North Slope whale hunters note that disturbed whales with altered surface behavior are difficult to hunt. To mitigate the impact of oil and gas activities on subsistence resources, significant effort over the last five decades has been made to better understand bowhead whale movements and feeding behavior in the Alaskan Beaufort Sea (Smultea et al., 2012).

Studies to determine the importance of the Alaskan Beaufort Sea as a feeding ground for bowhead whales have produced somewhat conflicting results. Feeding behavior has been regularly observed during aerial surveys in autumn (Würsig et al., 2002; Clarke et al., 2018) and occasionally in spring (Carroll et al., 1987; Mocklin et al., 2012). Analyses of stomach contents of harvested whales suggest that bowhead whales regularly find food in the Alaskan Beaufort Sea (Lowry and Burns, 1980; Lowry, 1993; Lowry et al., 2004). A study using isotopic signatures concluded that the Beaufort Sea is an important feeding area (Hoekstra et al., 2002) while another study also using isotopic signatures found that feeding in the Beaufort Sea contributes minimally to annual bowhead whale diet requirements (Lee et al., 2005). Additionally, bowhead whales are thought to require high densities of prey (Lowry, 1993; Thomson, 2002) that are not known to occur frequently in the Alaskan Beaufort Sea (Griffiths and Thomson, 2002). These seemingly conflicting results, among other reasons, prompted Alaska Natives to support and participate in the satellite telemetry study upon which this article is based.

During 2006–18, 89 bowhead whales were tagged with satellite transmitters in a collaborative study by the Alaska Department of Fish and Game, the Alaska Eskimo Whaling Commission, the North Slope Borough, whaling captains associations and partners in Canada (Department of Fisheries and Oceans Canada and the Tuktoyaktuk and Aklavik Hunters and Trappers Committees). This large, long-term telemetry dataset has provided new information on the movements, distribution, and behaviors of BCB bowhead whales. Tags on 67 of the 89 whales also provided data on dive behavior. Ten tags transmitted for over 365 days, providing information on year-round movements and behavior of individuals. Not all whale size (i.e., age) groups were equally represented in the sample, nonetheless, these data are useful to define bowhead whale core use areas throughout their range (i.e., hotspots that are likely feeding areas) (Citta et al., 2015). Results have also been used to more closely examine the relative importance and use of specific regions, including the Canadian Beaufort Sea (Harwood et al., 2017), the Chukchi Sea (Quakenbush et al., 2010; Citta et al., 2018), and the Bering Sea (Citta et al., 2012). The data further contributed to a better understanding of how whales alter their behavior relative to sea ice (Druckenmiller et al., 2018).

In this paper, we use the same 2006–18 telemetry dataset to examine movement behavior, residence times, and dive behavior of bowhead whales in three subregions of the Alaskan Beaufort Sea (Fig. 1). The western subregion, including Point Barrow, is a known bowhead whale feeding "hotspot" during the autumn migration in some years (Lowry and Frost, 1984; Ashjian et al., 2010; Citta et al., 2015; Clarke et al., 2017a). It provides a reference to compare bowhead whale movements and dive behavior with the central and eastern subregions, where their importance for feeding is less clear. We compare use of each subregion during the spring (April–May) and autumn (August–November) migratory periods and describe general use of the region during mid-summer (June–July). Bowhead whales are observed near Utqiaġvik (formerly Barrow) in mid-summer, but it is not known if these whales were returning from the Canadian Beaufort Sea prior to the main autumn migration or if they were arriving from the Chukchi Sea and did not make a prior spring migration to the Canadian Beaufort (Braham et al., 1980; Harwood et al., 2017). We explored the timing and duration of use of each subregion and used a two-state switching state-space model to infer bowhead whale behavior (transiting or lingering). We then examined dive data and hypothesized that areas of lingering are associated with feeding, which we determined by relating dive data to behavioral state. In addition to identifying behaviors associated with feeding, we also documented bowhead whale behavior and distribution within an area important for oil and gas development where active leases are located. Given the nutritional and cultural importance of bowhead whales to coastal Alaskan Native communities and the continued interest in offshore oil development for the region, it is important to better understand how bowhead whales use the Alaskan Beaufort Sea.

METHODS

Whale Tagging

From 2006–18, 89 bowhead whales from the BCB stock were tagged in three different regions: the Bering Sea (St. Lawrence Island), the Canadian Beaufort Sea (Tuktoyaktuk, Atkinson Point, Herschel Island, and Shingle Point), and the Alaskan Beaufort Sea (Point Barrow). Methods for tag deployment are detailed in Quakenbush et al. (2010) and Citta et al. (2015).

Whales were instrumented with a single SPOT, SPLASH, SPLASH10 (Wildlife Computers, Redmond, Washington), or CTD (conductivity, temperature, depth; Sea Mammal Research Unit, St. Andrews, Scotland) satellite tag. All tags provided animal location data when a whale surfaced and the tag antenna was above water (tags provided ~14 ± 12 raw locations day^{-1} [mean ± SD]). SPOT tags only provided location data. SPLASH tags and more recent SPLASH10 tags also provided dive data in the form of histograms. Histograms summarized 6-hour periods by collating dives into dive bins with different depth or time thresholds. Time-at-depth and maximum depth histograms collated dives into 14 depth bins with upper thresholds of 2, 10, 20, 30, 40, 50, 75, 100, 150, 200, 250, 300, 350, or depths over 350 m. Time-at-depth histograms recorded the proportion of a 6-hour period whales spent in each depth bin. Maximum depth histograms recorded the number of dives terminating in each depth bin. Dive duration histograms recorded the number of dives in different time bins; upper thresholds of the dive duration histograms were 6, 12, 18, 24, 30, 36, 42, 48, 54, 60, 66, 72, 78, or durations over 78 min. Because each 6-hour period in which dive behavior was summarized has an associated location estimate (see below), we linked dive depth to bathymetry. For histogram data, dives and times-at-depth where the bin threshold exceeded bottom depth were assumed to be benthic and were used to calculate the benthic dive rate and time spent at or near the seafloor. CTD tags provide information on individual dive duration and depth; however, these data are not summarized over 6-hour periods. We found that dive rate and time at depth estimated using CTD tag data was compromised by gaps in the data. Therefore, we limited analyses of whale dive behavior to histogram data derived from SPLASH and SPLASH10 tags only.

Location Processing and Behavioral State

Location data from the satellite tags are generated by the Argos satellite system and each location has an associated error that is used to assign that location to a quality class. Locations in classes 3, 2, or 1 have an associated error calculated by the Argos system, whereas error for locations in quality classes 0, A, or B must be estimated. Locations assigned to class Z are the least reliable and were removed from the dataset.

To obtain 6-hour location estimates that can be associated with dive histograms and to determine whale behavioral state, we fit a hierarchical, two-state switching, state-space model (sSSM) to our Argos data using the R package 'bsam' to fit our sSSM in a Bayesian framework (Jonsen et al., 2005; Jonsen, 2016). The sSSM model is particularly suited to our dataset because the hierarchical process allows for parameter estimates to be made across individuals, which improves the precision of the estimates, and error around Argos location estimates are modeled using t-distributions, which are more appropriate for Argos data (Jonsen, 2016). The sSSM is structured around a correlated random walk process, which estimates movement parameters for two inferred behavioral states (transiting or lingering) across all whales. The sSSM then applies these parameters to estimate individual whale locations given location error and to infer behavioral state at discrete time intervals (Jonsen et al., 2005, 2013; Jonsen, 2016). Whales that are *transiting* make direct movements and have longer step-lengths, whereas *lingering* whales change direction frequently and have shorter step-lengths. Using Markov chain Monte Carlo sampling, we estimated our posterior distributions using two chains with 50 000 iterations each. The first 10 000 iterations were discarded as the burn-in and posterior distributions were fit with the remaining 40 000 iterations in each chain. We assessed model convergence as described in Jonsen (2016). We estimated whale location and behavioral state at 6-hour intervals, representing a timestamp within 6-hour intervals in which dive behavior was summarized by SPLASH or SPLASH10 tags (0300 – 0900, 0900 – 1500, 1500 – 2100, 2100 – 0300 AKST). Before running the model, whale tracks were parsed into separate segments when gaps of more than two days occurred, and segments were only retained if they included raw location estimates for more than 15 days. Removing gaps and only retaining longer segments improved model convergence and the overall fit of the sSSM model. Final location estimates were only retained if they were within 24 hours of a raw location estimate.

Analysis

All statistical analyses were performed using R statistical software version 3.5.1 (R Core Team, 2018). Because sample sizes were generally small within years and inconsistent across years, we pooled the data and assigned year and individual within year as random effects for all analyses. We therefore made general inferences regarding bowhead whale use of the Alaskan Beaufort Sea during 2006 – 18.

We divided the Alaskan Beaufort Sea into three equidistant subregions by longitude and compared use by bowhead whales among them (Fig. 1). The eastern subregion was defined by the Alaska-Canada border on the east (−141˚ W) and extended to the western end of Camden Bay (−146˚ W). The central subregion extended from Camden Bay to the western end of the Colville River Delta, northwest of Nuiqsut (−151˚ W). The western subregion extended from the Colville River Delta to Point Barrow (−156˚ W). Each subregion was approximately 200 km wide. Oil and gas lease areas are present in the eastern and central subregions (Fig. 1). The Canadian Beaufort Sea is to the east of our study region and the Chukchi Sea is to the west.

We first compared the number of days tagged whales spent in each subregion during the spring (April – May) and autumn (August – November) migration periods. Mean residence time (days) within each subregion was calculated from whales with tracks traversing the entire Alaskan Beaufort in spring ($n = 16$) or autumn ($n = 23$). We used the data from our sSSM to determine the number of 6-hour periods (location estimates) for each whale within each subregion and used this number to calculate the mean number of days spent in each subregion during the spring and autumn migration periods. We then tested for differences in residence times between subregions within each season using a repeated-measures ANOVA (packages: lme4, lmerTest, functions: lmer, anova). For models that were significant, we used pairwise comparisons for mixed effect models (package: emmeans, function: emmeans) to determine which regions had significant differences.

We similarly used repeated measures ANOVA to compare both sea depth and distances from land at each estimated whale location between subregions and migratory seasons (spring and autumn) using our full dataset. Both sea depth and distance from land were log-transformed to better meet model assumptions (homoscedasticity and normality of residuals). For both responses, we tested for significant differences between subregions, season, and their interaction.

We then compared bowhead whale behavioral states between subregions and migratory season. Behavioral states were derived from our sSSM, which assigns each location estimate a behavioral state value between 0 and 1, representing the degree to which the whale's movements indicate lingering or transiting behavior. Values between 0 and 0.25 were considered transiting, and values between 0.75 and 1 were considered lingering. Locations with behavioral state values between 0.25 and 0.75 were not assigned a behavior and labeled as "uncertain." These locations were excluded from further analysis of behavior.

Using dive histograms, we compared four dive summary statistics to behavioral state (transiting or lingering) to test whether behavioral state was associated with different dive characteristics. We limited this analysis to the continental shelf (waters < 200 m deep) during the autumn migration. We tested for differences in whale dive rate (dives hr^{-1}), benthic dive rate (dives to seafloor hr^{-1}), the proportion of time below 10 m, and the proportion of time near the seafloor. We also tested for differences in dive duration between the two behavioral states by comparing the proportion of dives that were 0 – 6 min, 6 – 12 min, 12 – 18 min, 18 – 24 min, 24 – 30 min, or over 30 min in duration. We used repeated measures ANOVA to test for differences in each variable between the two behavioral states. We used a first-order autoregressive correlation structure (AR1) to account for temporal autocorrelation. We additionally compared our dive variables (dive rate, benthic dive rate, time below 10 m and time at the seafloor) among subregions using the same method described above. Dive data during the spring migration when bowhead whales were off the

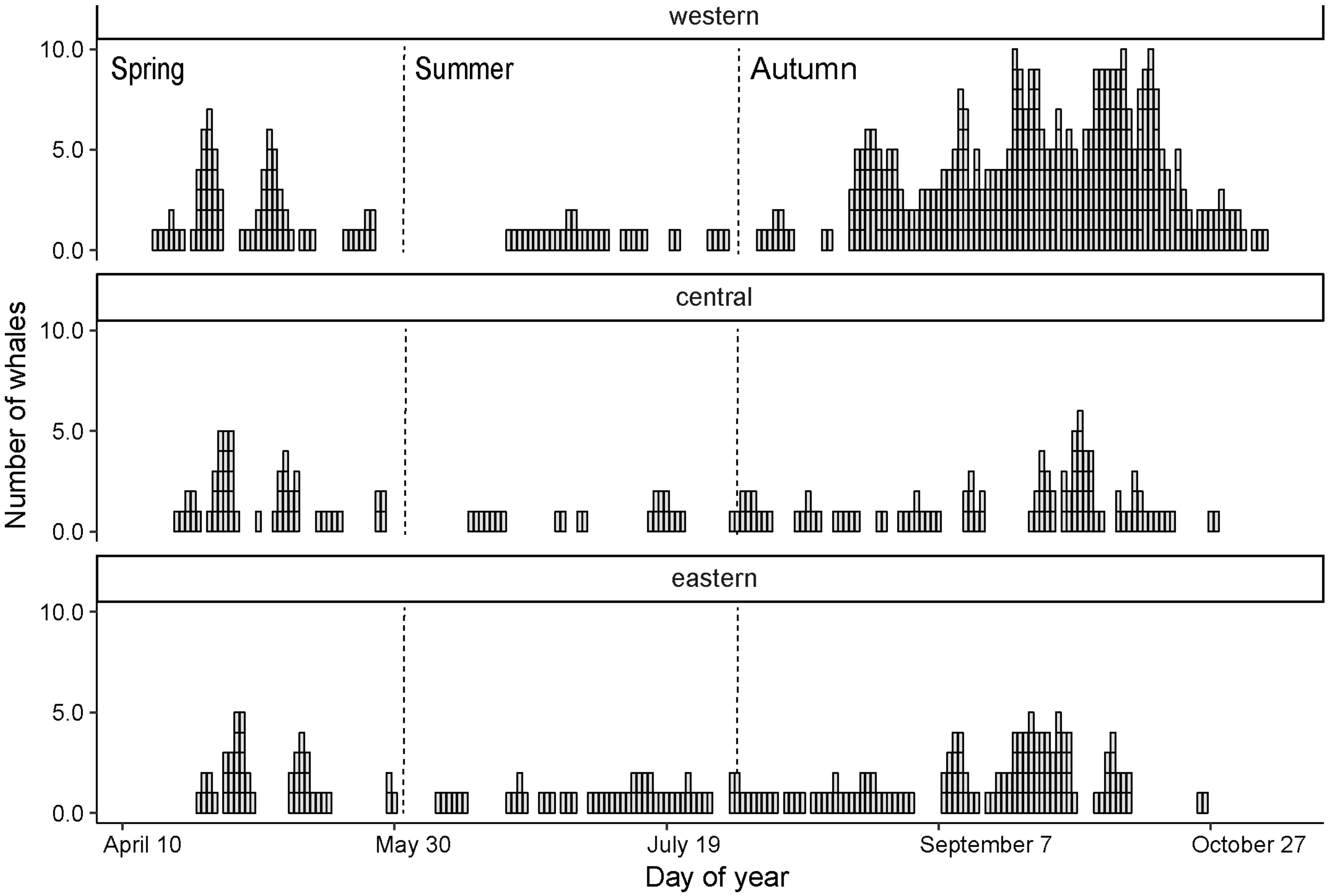

FIG. 2. Number of tagged whales per day in each region April–November. Data are pooled from all years (2006–18).

shelf was summarized but differences in dive behavior between behavioral states were not because lingering was rare during this time.

RESULTS

Of the 89 tagged whales, 48 whales had enough data for our sSSM, from which 3178 location estimates were generated in the Alaskan Beaufort Sea. Tagged whales first entered the Alaskan Beaufort Sea during the spring migration, migrating east from Point Barrow towards the Canadian Beaufort Sea. The earliest date a whale entered each subregion was 16 April for the western subregion, 19 April for the central subregion, and 24 April for the eastern subregion (Fig. 2). In autumn, as whales migrated west to the Chukchi Sea, the latest date a whale was present in each subregion was 26 October for the eastern subregion, 28 October in the central subregion, and 5 November for the western subregion (Fig. 2). In spring, individual whales tended to spend ~7 days traversing the Alaskan Beaufort, spending similar amounts of time in each subregion (Table 1; n = 16; F = 0.22; df = 2, 30; $p = 0.80$). In autumn, whales tended to spend ~19 days traversing the Alaskan Beaufort, spending twice as many days in the western subregion compared to the central and eastern subregions (n = 23; F = 8.22; df = 2, 44; $p < 0.001$). During the autumn migration, whales spent an average of ~4 days in each of the eastern and central subregions, but an average of ~10 days in the western subregion (Table 1).

Sea depths (F = 386.67; df = 2, 2742.7; $p < 0.001$) and distances from land (F = 209.85; df = 2, 2744.6; $p < 0.001$) at bowhead whale locations were significantly different depending on migratory season and subregion. During the spring migration, whales were closest to land while in the western subregion in shelf waters ~100 m deep (Table 2). As whales moved eastward, they left the continental shelf, traveling progressively farther from land and in deeper water (Fig. 3a). During the spring migration, most location estimates (78%) were off the continental shelf in deep water. In contrast, during the autumn migration, most whales traveled on the shelf in shallow water (Fig. 3c). Whales were closest to land in the eastern subregion but remained close to land while crossing the central and western subregions as well (Table 2). Two whales traversed the Alaskan Beaufort off the continental shelf in autumn, but only 10% of all location estimates during the autumn migration occurred off the shelf. One of the whales that migrated off the shelf in autumn followed the ice edge, traversing the Alaskan Beaufort Sea far north in the Arctic basin at latitudes greater than 76˚ N.

TABLE 1. Residence times (days) for bowhead whales in each equivalent size subregion during spring (n = 16, 2008–17) and autumn (n = 23, 2006–17) migration. Superscript letters denote significant differences between subregions within seasons.

	Western subregion	Central subregion	Eastern subregion	Total
Spring (April–May):				
Mean days ± SE	2.42 ± 0.16[a]	2.42 ± 0.16[a]	2.32 ± 0.16[a]	7.17 ± 0.41
Range	1.50, 3.25	1.75, 5.00	1.50, 4.25	4.75, 11.00
Median (days)	2.50	2.25	2.12	6.87
Proportion ± SE	0.34 ± 0.01	0.34 ± 0.01	0.32 ± 0.01	–
Autumn (August–November):				
Mean days ± SE	10.05 ± 1.22[a]	4.05 ± 1.22[b]	4.55 ± 1.22[b]	18.66 ± 2.30
Range	1.75, 35.00	1.00, 15.50	1.25, 13.75	4.75, 47.50
Median (days)	9.37	5.12	5.12	16.50
Proportion ± SE	0.50 ± 0.04	0.24 ± 0.03	0.25 ± 0.02	–

TABLE 2. Distance from land and sea depths used by bowhead whales by subregion and season. Superscript letters denote significant differences between subregions within seasons.

		Western subregion	Central subregion	Eastern subregion
Distance (km)	Spring	36.06 ± 0.001[a]	70.63 ± 0.001[b]	88.67 ± 0.001[c]
	Autumn	26.05 ± 0.001[a]	23.31 ± 0.001[a]	12.82 ± 0.001[b]
Depth (m)	Spring	−98.35 ± 1.21[a]	−1078.85 ± 1.21[b]	−1360.33 ± 1.21[b]
	Autumn	−41.48 ± 1.19[a]	−35.64 ± 1.20[a,b]	−29.30 ± 1.20[b]

During the spring migration, tagged whales rarely exhibited lingering behavior (Fig. 4a). Some location estimates were classified as lingering during the spring migration for the western (10%) and central (11%) subregions (Table 3), but they were all from 1 of 26 whales that were in the Alaskan Beaufort Sea in spring. Tagged whales did not linger in the eastern subregion during the spring migration. In autumn, migrating whales infrequently lingered in the eastern (17%) and central (8%) subregions. However, in autumn, nearly half of all location estimates in the western subregion were classified as lingering (47%, 24 of 43 whales that were in the Alaskan Beaufort Sea) (Table 3, Fig. 4c).

A small number of tagged whales (n = 7) spent time in the Alaskan Beaufort Sea during June and July (Fig. 3b), when most whales were farther east in the Canadian Beaufort. All whales present during this time arrived from the Canadian Beaufort, and most (n = 5) looped back eastward to Canadian waters after traveling varying distances westward. One of these whales traveled as far west and north as Wrangel Island, Russia, and then looped back to the Canadian Beaufort. Of the two whales that did not loop back to the Canadian Beaufort, one traversed the Chukchi Sea to the northern coast of Chukotka, Russia, and the other stopped transmitting after traveling far north of Wrangel Island in the Arctic basin but was heading east again when transmission ceased. Whales that visited the Alaskan Beaufort during the summer tended to stay off the shelf except for the one whale that left the Beaufort for the Chukotka Peninsula during this time (Fig. 3b). Two whales that engaged in lingering behavior during the summer were off the shelf in deep water and another whale lingered on the shelf near the Canadian border (Fig. 4b). One whale that lingered off the shelf primarily dove to depths of 10–75 m when lingering, while the second whale had no dive data available. The whale that lingered on the shelf made both mid-water dives (10–30 m) and dives to the seafloor (40–50 m).

During autumn on the continental shelf, lingering and transiting whales exhibited statistically significant differences in their dive behavior (Fig. 5). Lingering whales had greater dive rates (4.35 ± 0.47 versus 3.61 ± 0.46 dives hr^{-1} (mean ± SE); F = 9.22; df = 1, 475; p = 0.002) and benthic dive rates (3.72 ± 0.50 versus 2.78 ± 0.50 benthic dives hr^{-1}; F = 14.31; df = 1, 475; $p < 0.001$), but spent less time below 10 m (proportion of time: 0.52 ± 0.03 versus 0.62 ± 0.03; F = 14.17; df = 1, 504; $p < 0.001$). Despite spending less time below 10 m, there was no difference in time spent near the seafloor between lingering and transiting whales (proportion of time: 0.45 ± 0.07; F = 0.15; df = 1, 504; p = 0.69). There was no difference between subregions for whale dive rate (F = 0.83; df = 2, 474; p = 0.43), benthic rate (F = 1.87; df = 2, 474; p = 0.15), time below 10 m (F = 0.28; df = 2, 503; p = 0.75), or time at the seafloor (F = 0.04; df = 2, 503; p = 0.95). In spring, whales that were off the shelf did not dive to the seafloor. During the spring migration, average dive rate was 3.58 ± 0.31 dives hr^{-1}, and whales spent most of their time below 10 m (proportion of time: 0.74 ± 0.04) (Fig. 5).

Differences in dive duration were subtle between behavioral states (Fig. 6). On the continental shelf in autumn, the proportion of dives 0–6 min long was equivalent for both lingering and transiting whales (proportion of dives: 0.40 ± 0.13; F = 0.07; df = 1, 472; p = 0.78). Lingering whales engaged in more dives 6–12 min in length (0.17 ± 0.02) than transiting whales (0.12 ± 0.02) (F = 8.09; df = 1, 472; p = 0.004). The proportion of dives 12–18 min in length were equivalent for both behavioral states (0.12 ± 0.02; F = 0.002; df = 1, 472; p = 0.96). Transiting whales dove for 18–24 min (0.11 ±

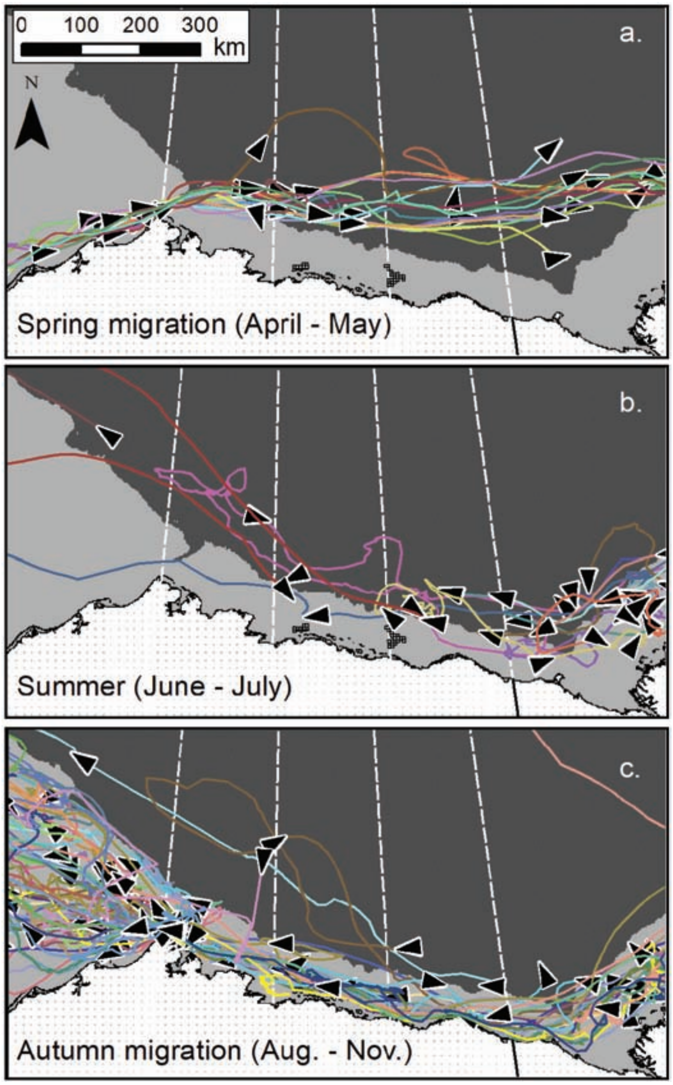

FIG. 3. Direction of travel and estimated tracks for 48 bowhead whales that used the Alaskan Beaufort Sea, 2006–18, during spring (a), summer (b), and autumn (c). Colors correspond to individual whales.

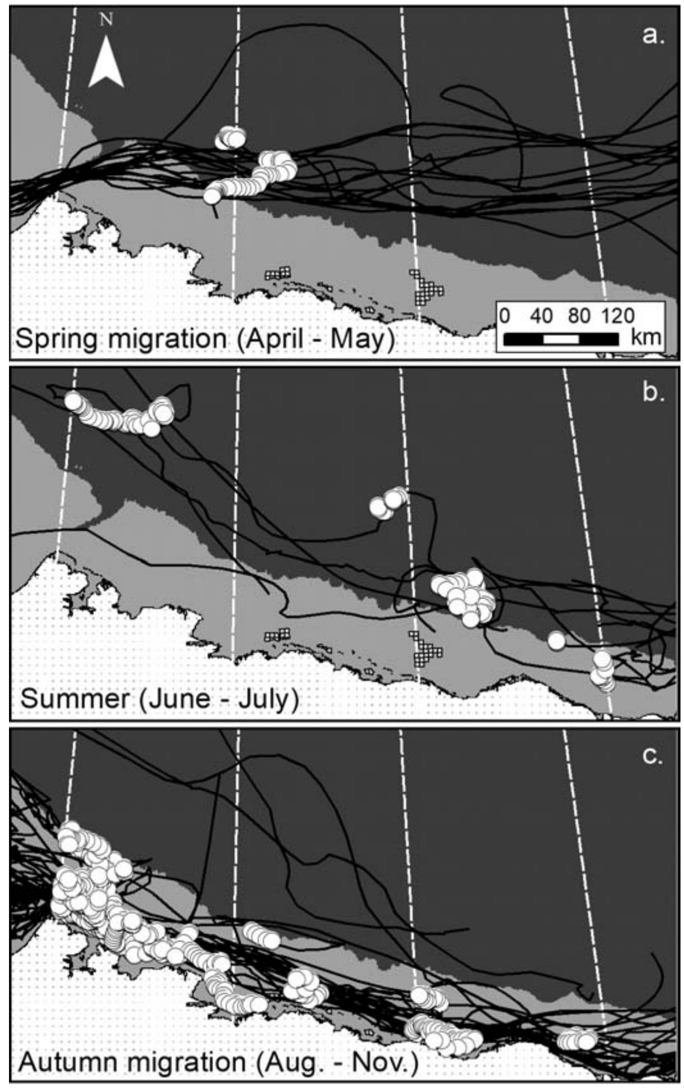

FIG. 4. Locations where bowhead whales lingered (white circles) as determined by a two-state switching, state space model (sSSM) for spring (a), summer (b), and autumn (c).

TABLE 3. Percentage of location estimates classified as lingering, transiting, or uncertain for each subregion within the spring (April–May) and autumn (August–November) migratory seasons.

Season	Subregion	% Lingering	% Transiting	% Uncertain	Number of locations (whales)
Spring	Western	10	81	8	228 (19)
	Central	11	82	7	189 (19)
	Eastern	0	96	4	173 (17)
Autumn	Western	47	29	24	1423 (43)
	Central	8	78	13	373 (23)
	Eastern	17	64	18	419 (23)

0.04) more than lingering whales (0.09 ± 0.04) (F = 9.62; df = 1, 472; p = 0.002). There was no difference in the proportion of dives that were 24–30 min (~0.13 ± 0.06; F = 0.85; df = 1, 472; p = 0.35) or over 30 min (~0.11 ± 0.08; F = 3.11; df = 1, 472; p = 0.08). During the spring migration, most dives were 0–6 min long (0.62 ± 0.03) (Fig. 6). Whales also made dives 6–12 min (0.13 ± 0.04) and 12–18 min long (0.10 ± 0.02). Unlike dives in autumn, whales infrequently made dives 18–24 min (0.06 ± 0.01), 24–30 min (0.04 ± 0.01), or over 30 min (0.05 ± 0.03) during the spring migration.

Throughout this study, 19 whales passed within 10 km of areas leased for oil and gas activities and had tracks, estimated from the sSSM that passed through them. Three of these whales lingered near the oil leases (Fig. 7). When viewing raw location data, 83 locations for 14 whales were within leased areas.

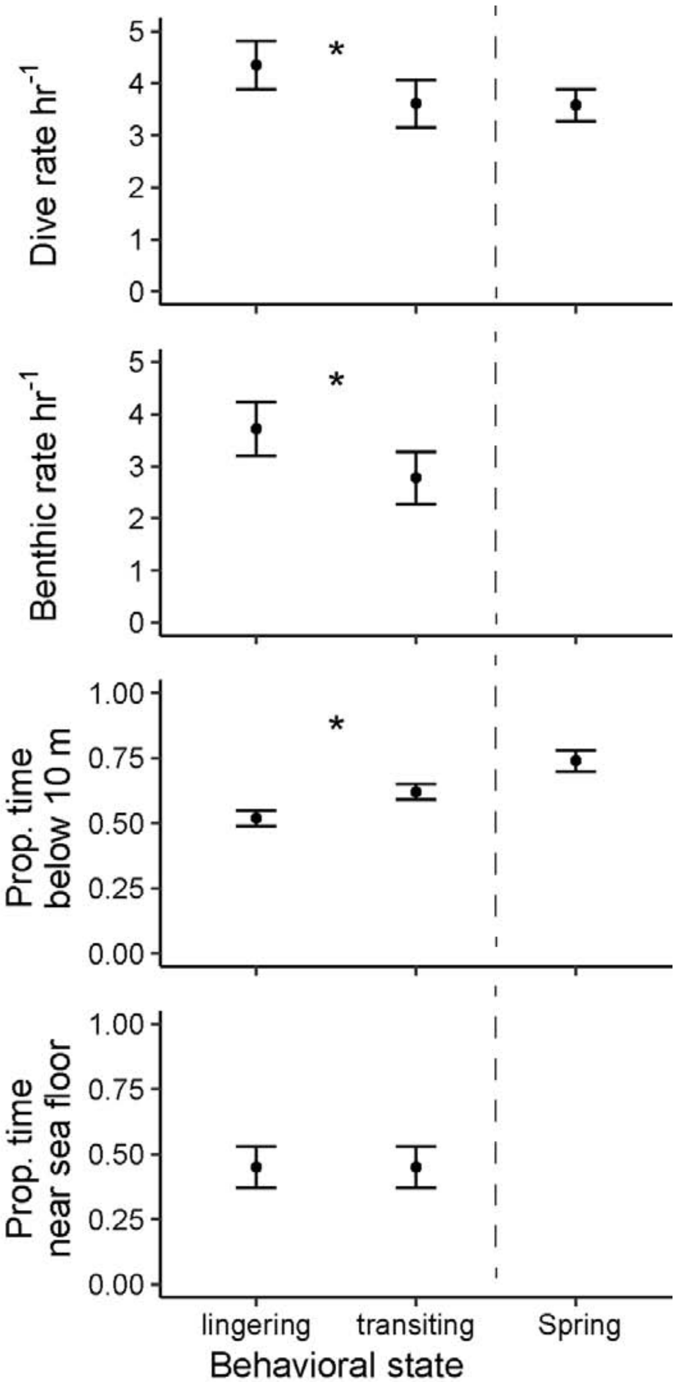

FIG. 5. Dive variables in relation to whale behavioral state during the autumn migration on the continental shelf and during the spring migration in the Arctic basin when whales were mainly transiting. Asterisks denote significant differences between behavioral states during the autumn migration. Error bars represent the standard error.

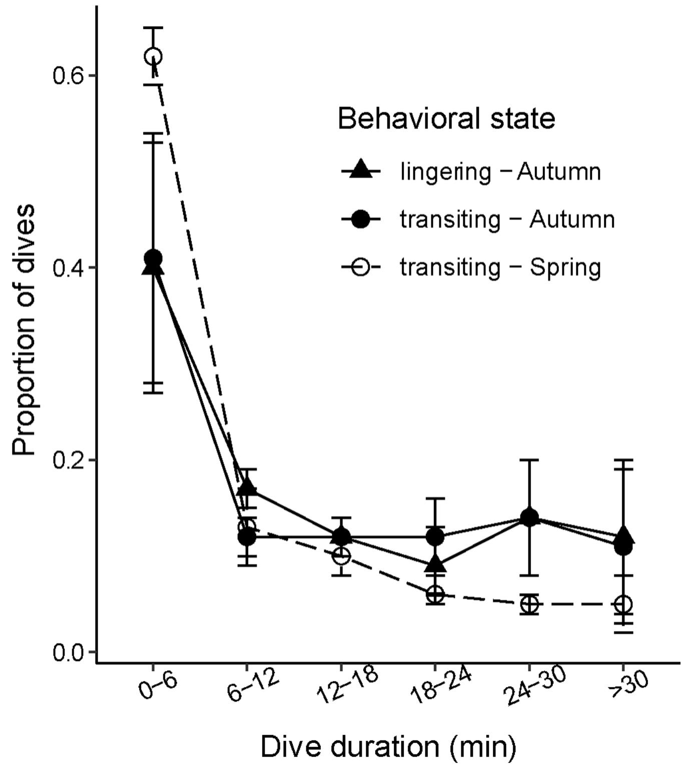

FIG. 6. Proportion of dives by dive duration for each behavioral state during the spring and autumn migrations. Note that lingering during spring was too rare to plot.

DISCUSSION

Bowhead whale behavior was clearly different during the spring and autumn migrations through the Alaskan Beaufort Sea. These differences are most likely attributable to whales making a sustained migration eastward through the Alaskan Beaufort in spring and lingering to forage as they migrate westward through the region in autumn.

Spring Behavior

In spring, whales migrated quickly across the Alaskan Beaufort, traversing the entire region in ~7 days and each subregion in ~2 days (Table 1). Other observations of whale residence times in the Alaskan Beaufort during the spring migration are unavailable, however, prior studies often report observed travel rates of whales during this time. For bowhead whales to traverse the Alaskan Beaufort in ~7 days would require an average travel rate of ~3 – 4 km hr^{-1}, which is equivalent to an estimate of spring migration travel rates derived from aerial photography (4.0 km hr^{-1}, Rugh, 1990). Rugh and Cubbage (1980) observed whales passing Cape Lisburne, Alaska, at an average rate of 4.7 ± 0.6 km hr^{-1}, prior to entering the Alaskan Beaufort during the spring migration, and Carroll and Smithhisler (1980) observed travel rates of 1 – 11 km hr^{-1} near Point Barrow. The most extensive data on swim speeds during spring migration were derived from ice-based surveys and suggest speeds of 3 – 4 km hr^{-1} (Zeh et al., 1993). Combined, these studies suggest that bowhead whales have crossed the Alaskan Beaufort at similar travel rates through time, and thus had similar short residence times, during the spring migration.

Most whale dives in spring were of short duration (< 6 min; Fig. 6). Diving while traveling in spring is likely because bowhead whales are primarily transiting under heavy pack ice during the spring migration (Braham et al., 1980; George et al., 1989). If pack ice extends several meters below the surface, traveling under ice may also

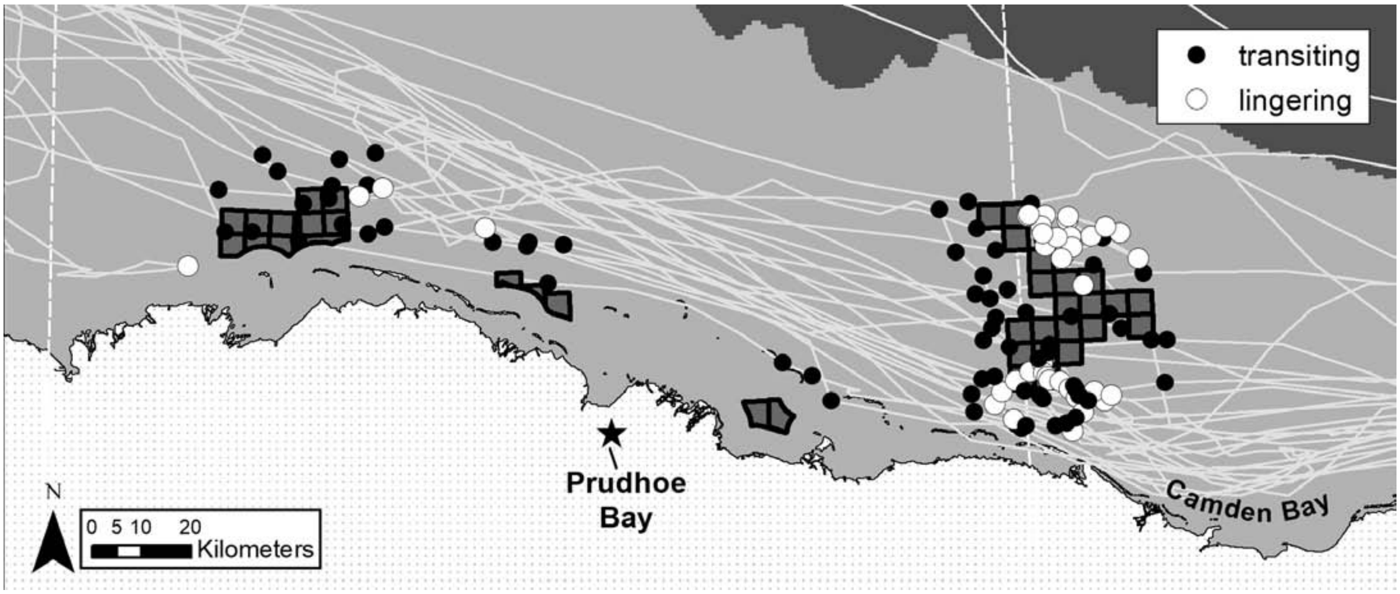

FIG. 7. Bowhead whale tracks (light grey lines) and locations (circles, 19 whales) within 10 km of oil and gas leased areas (dark grey blocks) during the autumn migration in the Alaskan Beaufort Sea across all years (2006–18).

cause whales to spend most of their time below 10 m (Fig. 5). Swimming at greater depths may also be more efficient than swimming near the surface because of hydrodynamic drag (Williams, 2002). Because whales are mainly traveling over the basin in deep water during spring (Table 2; Fig. 3a), they do not dive to the seafloor and may be less likely to encounter concentrated prey than when traveling over shallower shelf waters.

Bowhead whales are occasionally known to feed in the western subregion during spring (Carroll et al., 1987; Lowry et al., 2004; Mocklin et al., 2012). Lowry et al. (2004) found that 34% (31 of 91) of whales sampled during the spring harvest at Utqiaġvik showed some evidence of feeding, and Mocklin et al. (2012) reported that 55% of aerial photos of whales near Point Barrow in May showed evidence of feeding near the seafloor (i.e., mud on their heads). However, the quantity of food in the stomach of whales sampled in spring tends to be much less than in autumn (Lowry et al., 2004) when their forestomachs are often full to capacity (North Slope Borough, unpubl. data). Tagged whales in our study rarely lingered during spring, suggesting that prey densities did not warrant pausing their migration to the Canadian Beaufort. Only a single whale exhibited lingering behavior during the spring migration, and this occurred in deep water. The few dive records available for this whale while it lingered showed that it spent considerable time at the surface (> 10 m), which could reflect feeding, resting, or be a response to ice conditions (Würsig and Clark, 1993). For one 6-hour period, this whale dove to depths of 100–250 m, where the Polar halocline separating Pacific Water from Atlantic Water in spring has been reported (Pickart, 2004). Because zooplankton prey may be concentrated by the halocline (e.g., Citta et al., 2013; Hauser et al., 2015; Stafford et al., 2016), this whale may have been feeding at this time. Hence, while whales are known to feed during the spring migration, it is likely that most often zooplankton densities have not yet developed to the extent sufficient to warrant whales pausing their migration long enough to be detected by satellite telemetry and our definition of lingering. Prey densities (euphausiids) tend to increase in the Alaskan Beaufort after the spring migration period (Berline et al., 2008).

Autumn Behavior

Compared to the spring migration, whales migrated slowly across the Alaskan Beaufort during the autumn migration, averaging ~19 days to traverse the region. In autumn, whales spent nearly double the amount of time in the eastern and central subregions than in spring and triple the amount of time in the western subregion than in spring (Table 1). Würsig et al. (2002) estimated from aerial surveys that whales spend ~4 days in the eastern subregion, similar to our satellite telemetry results. Mate et al. (2000) tracked the movements of an individual bowhead whale across the Alaskan Beaufort Sea and also found that whale spent ~4 days in the eastern subregion. This whale only spent ~3–4 days in the central subregion and ~3 days in the western subregion, which are shorter durations than most whales in our study spent in these subregions (Table 1). Additional estimates for duration spent in the central and western subregions by individual whales are not available. It is possible that the longer residence times we observed for each subregion during the autumn migration versus the spring migration are partly due to social interactions, however, social behavior is considered less common in autumn (Würsig and Clark, 1993). More likely, longer residence times reflect that whales are searching for food or feeding in addition to migrating.

The dive data and the frequency of lingering behavior support the assumption that longer residence times during the autumn migration are associated with more feeding at that time. Most differences in dive patterns between behavioral states are likely not biologically significant, despite statistical significance. Rather, whales in our dataset maintained a dive behavior throughout the autumn migration consisting of frequent diving to the seafloor, irrespective of behavioral state. When on the shelf, whales consistently spent 45% of their time near the seafloor (Fig. 5) where their primary prey (copepods and euphausiids) are known to concentrate (Ashjian et al., 2010; Walkusz et al., 2012). Whales also engaged in more long duration dives in autumn than in spring (~34% versus ~15% of dives were > 18 min; Fig. 6). Longer duration dives at the seafloor may reflect feeding as bowhead whales must swim slowly when filtering zooplankton with mouths slightly open (Lowry, 1993). If whales are constantly searching for food near the seafloor, then dive behavior may be similar within each behavioral state, as we observed. The main difference will be that whales pause migration to feed when sufficient densities of prey are located (i.e., linger), which primarily occurred during the autumn migration in the western subregion (Table 3).

Diving to the seafloor throughout their autumn migration suggests that whales are continuously looking for food. This behavior is reasonable given the known patchiness of their zooplankton prey (Griffiths and Thomson, 2002). In the eastern and central subregions, dense aggregations of prey suitable for bowhead feeding occurs infrequently (Okkonen et al., 2018). Given the longevity of bowhead whales (George et al., 1999), which itself may be an adaptation to relatively low prey densities and intermittent feeding opportunities, it is reasonable to assume that a collective memory of these infrequent events motivates whales to continuously look for food while passing through the eastern and central subregions, despite good feeding opportunities being rare (i.e., those warranting pausing their migration). Data from analyses of stomach contents showed that over 75% of sampled stomachs from harvested whales at Kaktovik (eastern subregion) and Cross Island (central subregion) contained some prey items, suggesting that whales do find food in these areas (Lowry et al., 2004). Aerial surveys also suggest that feeding in the eastern and central subregions is patchy and ephemeral; where whales aggregated and the number of observations of whales feeding varied substantially year to year (Clarke et al., 2018). One notable example of these rare feeding events occurred in August 2016 when more than 400 bowhead whales were observed feeding in Harrison Bay (in the central subregion) during aerial surveys (Clarke et al., 2017b). Whales lingered in the autumn within the western subregion more frequently, because unlike the eastern and central subregions, prey (euphausiids) is more frequently concentrated into dense aggregations by a process of consistent upwelling winds followed by calm winds known as the "krill trap" (Ashjian et al., 2010; Citta et al., 2015; Okkonen et al., 2018). Consistent upwelling winds also drive copepods onto the shelf where they aggregate north of the Tuktoyaktuk Peninsula and west of Cape Bathurst in the Canadian Beaufort Sea (Walkusz et al., 2012), which are other bowhead whale hotspots (Citta et al., 2015; Harwood et al., 2017). Relative to these hotspots, the eastern and central subregions within the Alaskan Beaufort Sea appear to be less important feeding areas for the population of BCB whales, in part because average prey densities are probably lower (Griffiths and Thomson, 2002; Walkusz et al., 2012).

Some whales (n = 7) also spent time in the Alaskan Beaufort during summer. All of these whales had migrated first to the Canadian Beaufort in spring before turning around and then reentering the Alaskan Beaufort for variable lengths of time in summer. We therefore consider it likely that whales observed north of Utqiaġvik in July arrived from the Canadian Beaufort rather than the Chukchi Sea. Interestingly, nearly all these whales then looped back to the Canadian Beaufort before migrating across the Alaskan Beaufort once more during the autumn migration.

Oil and gas leases in the Alaskan Beaufort are in areas used by bowhead whales during their autumn migration. Several whales passed through or within 10 km of lease blocks. Three whales lingered and were thus likely feeding near lease blocks for 1, 4, and 5 days (Fig. 7). It is also notable that the majority of whales appeared to migrate south of the lease blocks, between them and the barrier islands just west of Camden Bay, an area ~10 km wide (Fig. 7).

Importance of the Alaskan Beaufort Sea

The Alaskan Beaufort Sea is clearly important for migrating bowhead whales. There are approximately 17 000 BCB bowhead whales (Givens et al., 2016), the majority of which migrate through the Alaskan Beaufort Sea twice each year. Fewer than 1000 whales are thought to summer in the Chukchi Sea and not pass through the Alaskan Beaufort Sea (Melnikov and Zeh, 2007). Likewise, the Alaskan Beaufort Sea is clearly important for the whaling communities that rely on bowhead whales for subsistence (Stoker and Krupnik, 1993).

Determining how important the Alaskan Beaufort Sea is as a feeding area for bowhead whales is much more difficult. That bowhead whales feed in the Alaskan Beaufort Sea is indisputable and although feeding may be less common during the spring migration, feeding during the autumn migration is well documented via aerial surveys (e.g., Würsig et al., 2002; Clarke et al., 2018) and by examination of stomach contents (Lowry and Burns, 1980; Lowry et al., 2004). However, comparable data are incomplete across the remainder of the range and the occurrence of feeding is largely unknown away from whaling villages or outside the range of aerial surveys. Although isotope studies suggest feeding generally occurs year-round (e.g., Hoekstra et al., 2002; Pomerleau et al., 2018), determining exactly where feeding occurs and to what extent are difficult.

If we assume that longer residence times and more lingering behavior by satellite-tagged individuals are indicators of prey density and the level of feeding (and probably nutritional gain), then we would conclude that while feeding occurs within the Alaskan Beaufort Sea, much more feeding occurs elsewhere. For example, in spring, tagged bowhead whales (n = 22) spent an average of 52 days in a 200 km area surrounding Cape Bathurst in the Canadian Beaufort Sea, and 50% of location estimates in this area were classified as lingering. Near Serdtse-Kamen on the Russian coast in the Chukchi Sea, tagged bowhead whales (n = 33) spent an average of 32 days in a 200 km area during late fall and early winter. A third of those location estimates were classified as lingering. Although these areas are roughly equivalent in size to the subregions in the Alaskan Beaufort Sea, these mean residence times are ~8–12 times longer than autumn mean residence times for the eastern and central subregions, and ~3–5 times longer than for the western subregion (Alaska Department of Fish and Game, unpubl. data). Although feeding occurs in the Alaskan Beaufort Sea, other regions, where more feeding appears to take place, likely contribute more to the annual energy budget of bowhead whales. In summary, no single definitive tool exists for determining the relative importance of feeding across the BCB range, however, the weight of evidence based on telemetry, aerial surveys, isotopic data, stomach examinations, commercial whaling records (Bockstoce et al., 2005), and low overall productivity of the Alaskan Beaufort Sea (Niebauer and Schell, 1993; Griffiths and Thomson 2002) supports the conclusion that the Alaskan Beaufort Sea is less important nutritionally than other regions of their range. Nonetheless, the region is extremely important as a bowhead migratory corridor and subsistence whaling area, making it difficult to rank its overall importance.

CONCLUSION

In spring, the Alaskan Beaufort Sea was primarily a migratory corridor with little evidence of lingering (presumably feeding), for BCB bowhead whales in our study. Although whales were not likely feeding during this time, the need to cross this region to access summering grounds means it is of great importance to whales (Quakenbush et al., 2010). In autumn, the Alaska Beaufort Sea shelf was a migratory corridor in which whales sometimes paused migratory movements, presumably to feed. Behavior consistent with feeding was most common in the western subregion, near Utqiaġvik. During the autumn migration, bowhead whales engaged in long dives to the seafloor, behavior that suggests whales were consistently looking for prey as they migrated. In the central and eastern subregions, migrating whales rarely paused migrating long enough to be detected by satellite telemetry (likely ≥ 1 day in duration), suggesting that prey concentrations do not commonly warrant pausing migratory movements.

The Arctic is in a period of rapid change with rising water temperatures (Wood et al., 2013) and declines in the extent of sea ice and the duration of ice coverage (Wang et al., 2018). It is reasonable to assume that how bowhead whales use the Alaskan Beaufort Sea will also change. Shifts in the timing of use of the Alaskan Beaufort by bowhead whales are already being detected from aerial surveys spanning four decades (Clarke et al., 2018). While we do not foresee the importance of the Alaskan Beaufort as a migratory corridor for bowhead whales and as a hunting ground for Alaska Natives diminishing, we expect that primary productivity and patterns of upwelling will change, in turn changing how frequently bowhead whales forage in the region. As such, the patterns we have documented may already be outdated.

ACKNOWLEDGEMENTS

This project was highly cooperative and involved contributions from many organizations, agencies, and individuals, including the following: Alaska Eskimo Whaling Commission (the late Arnold Brower, Sr., Harry Brower, Jr., Ray Koonooka, George Noongwook, Merlin Koonooka), North Slope Borough (Billy Adams, Qaiyaan Leavitt, Bobby Sarren, Robert Suydam, Taqulik Hepa), Barrow and Kaktovik Whaling Captain's Associations (Eugene Brower, Charlie Hopson, Lloyd Hopson, Carl Nayakik, Jared Nayakik, Mike Donovan, Jordan Kippi, Justin Gatten, Fenton Rexford, Joe Kaleak, George Tagarook, and Eddie Arey), Barrow Arctic Science Consortium (Lewis Brower), St. Lawrence Island crews (Thomas Akeya, Carl Pelowook, Clarence Irrigoo, and Edgar Campbell), Aklavik and Tuktoyaktuk Hunters and Trappers Committees (Charles Pokiak, James Pokiak, Gary Raddi, Sr., Gary Raddi, Jr., Sammy Gruben, Joseph Felix, Jr., Raymond Ettagiak, Dennis Arey, Larry Arey, Pat Kasook, Buddy Gruben, Douglas Panaktalok, Mikkel Panaktalok, Max Kotokak, Sr.), Department of Fisheries and Oceans Canada (DFO) (Kevin Bill, Tim Leblanc, Patrick Ryan, Terry Stein, Angus Alunik, and Kate Snow), Dr. Stephen Raverty of the British Columbia Animal Health Center, and Mikkel and Anders Jensen of the Greenland Institute of Natural Resources. Captain Michael Fleming and R/V *Ukpik* provided vessel support in Canada. We appreciate Robert Small's lead of the early Canadian field efforts. Funding for tagging efforts was mainly provided by U.S. Minerals Management Service (now Bureau of Ocean Energy Management) under contracts M12PC00005, M10PC00085, and M05PC00020, with support and assistance from Charles Monnett, Jeffery Denton, Carol Fairfield, and Heather Crowley. Work in Canada was also funded by the Fisheries Joint Management Committee, Ecosystem Research Initiative (DFO), and Panel for Energy Research and Development. CTD tags, their deployments, and analysis were funded by the U.S. Office of Naval Research, with the support and assistance of Michael Weise under contract N00014-16-1-3019. Bowhead whale research has been conducted in the U.S. under research permits issued to the National Marine Fisheries Service (No. 782-1719) and to the Alaska Department of Fish and Game (ADFG) (Nos. 14610 and 18890) and under ADFG

Animal Care and Use permit Nos. 06-16, 09-21, 10-13R, 12-020, 2013-20, 2014-03, 2015-25, 2016-23, 0027-2017-27, 0027-2018-29. In Canada, research was conducted under Department of Fisheries and Oceans Scientific License Nos. S-07/08-4007-IN, S-08/09-4000-IN, S-09/10-4005-IN-A1, S-14/15-1027-NU, S-16/17-3035-YK, and S-17/18-3034-YK, and Animal Care Protocols FWI-ACC-2007-2008-013, FWI-ACC-2008-031, FWISL-ACC-2009-019, AUP 2010-034, AUP 2014-048, AUP 2016-045, and AUP-2017-35.

REFERENCES

Ashjian, C.J., Braund, S.R., Campbell, R.G., George, J.C., Kruse, J., Maslowski, W., Moore, S.E., et al. 2010. Climate variability, oceanography, bowhead whale distribution, and Iñupiat subsistence whaling near Barrow, Alaska. Arctic 63(2):179–194.
https://doi.org/10.14430/arctic973

Berline, L., Spitz, Y.H., Ashjian, C.J., Campbell, R.G., Maslowski, W., and Moore, S.E. 2008. Euphausiid transport in the western Arctic Ocean. Marine Ecology Progress Series 360:163–178.
https://doi.org/10.3354/meps07387

Bockstoce, J.R., Botkin, D.B., Philp, A., Collins, B.W., and George, J.C. 2005. The geographic distribution of bowhead whales, *Balaena mysticetus*, in the Bering, Chukchi, and Beaufort Seas: Evidence from whaleship records, 1849–1914. Marine Fisheries Review 67(3):1–43.

Braham H.W., Fraker, M.A., and Krogman, B.D. 1980. Spring migration of the western Arctic population of bowhead whales. Marine Fisheries Review 42(9-10):36–46.

Braund, S.R., and Kruse, J., eds. 2009. Synthesis: Three decades of research on socioeconomic effects related to offshore petroleum development in coastal Alaska. Anchorage: U.S. Department of the Interior, Minerals Management Service.

Carroll, G.M., and Smithhisler, J.R. 1980. Observations of bowhead whales during spring migration. Marine Fisheries Review 42(9-19):80–85.

Carroll, G.M., George, J.C., Lowry, L.F., and Coyle, K.O. 1987. Bowhead whale (*Balaena mysticetus*) feeding near Point Barrow, Alaska, during the 1985 spring migration. Arctic 40(2):105–110.
https://doi.org/10.14430/arctic1754

Citta, J.J., Quakenbush, L.T., George, J.C., Small, R.J., Heide-Jørgensen, M.P., Brower, H., Adams, B., and Brower, L. 2012. Winter movements of bowhead whales (*Balaena mysticetus*) in the Bering Sea. Arctic 65(1):13–34.
https://doi.org/10.14430/arctic4162

Citta, J.J., Suydam, R.S., Quakenbush, L.T., Frost, K.J., and O'Corry-Crowe, G.M. 2013. Dive behavior of eastern Chukchi beluga whales (*Delphinapterus leucas*), 1998–2008. Arctic 66(4):389–406.
https://doi.org/10.14430/arctic4326

Citta, J.J., Quakenbush, L.T., Okkonen, S.R., Druckenmiller, M.L., Maslowski, W., Clement-Kinney, J., George, J.C., et al. 2015. Ecological characteristics of core-use areas used by Bering–Chukchi–Beaufort (BCB) bowhead whales, 2006–2012. Progress in Oceanography 136:201–222.
https://doi.org/10.1016/j.pocean.2014.08.012

Citta, J.J., Okkonen, S.R., Quakenbush, L.T., Maslowski, W., Osinski, R., George, J.C., Small, R.J., Brower Jr., H., Heide-Jørgensen, M.P., and Harwood, L.A. 2018. Oceanographic characteristics associated with autumn movements of bowhead whales in the Chukchi Sea. Deep Sea Research Part II: Topical Studies in Oceanography 152:121–131.
https://doi.org/10.1016/j.dsr2.2017.03.009

Clarke, J.T., Brower, A.A., Ferguson, M.C., and Willoughby, A.L. 2017a. Distribution and relative abundance of marine mammals in the eastern Chukchi and western Beaufort Seas, 2015. Annual Report, OCS Study BOEM 2017-019. National Marine Mammal Laboratory, Alaska Fisheries Science Center.
https://www.boem.gov/newsroom/library/scientific-and-technical-publications-2017

———. 2017b. Distribution and relative abundance of marine mammals in the eastern Chukchi and western Beaufort Seas, 2016. Annual Report, OCS Study BOEM 2017-078. Seattle, Washington: National Marine Mammal Laboratory, Alaska Fisheries Science Center.
https://doi.org/10.7289/V5HX1B11

Clarke, J.T., Ferguson, M.C., Willoughby, A.L., and Brower, A.A. 2018. Bowhead and beluga whale distributions, sighting rates, and habitat associations in the western Beaufort Sea in summer and fall 2009–16, with comparison to 1982–91. Arctic 71(2):115–138.
https://doi.org/10.14430/arctic4713

Clarke, J.T., Brower, A.A., Ferguson, M.C., and Willoughby, A.L. 2019. Distribution and relative abundance of marine mammals in the eastern Chukchi and western Beaufort Seas, 2018. Annual Report, OCS Study BOEM 2019-021. Seattle, Washington: National Marine Mammal Laboratory, Alaska Fisheries Science Center.

Druckenmiller, M.L., Citta, J.J., Ferguson, M.C., Clarke, J.T., George, J.C., and Quakenbush, L. 2018. Trends in sea-ice cover within bowhead whale habitats in the Pacific Arctic. Deep Sea Research Part II: Topical Studies in Oceanography 152:95–107.
https://doi.org/10.1016/j.dsr2.2017.10.017

George, J.C., Clark, C., Carroll, G.M., and Ellison, W.T. 1989. Observations on the ice-breaking and ice navigation behavior of migrating bowhead whales (*Balaena mysticetus*) near Point Barrow, Alaska, spring 1985. Arctic 42(1):24–30.
https://doi.org/10.14430/arctic1636

George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T., and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. Canadian Journal of Zoology 77(4):571–580.
https://doi.org/10.1139/z99-015

Givens, G.H., Edmonson, S.L., George, J.C., Suydam, R., Charif, R.A., Rahaman, A., Hawthorne, D., Tudor, B., DeLong, R.A., and Clark, C.W. 2016. Horvitz-Thompson whale abundance estimation adjusting for uncertain recapture, temporal availability variation, and intermittent effort. Environmetrics 27(3):134–146.
https://doi.org/10.1002/env.2379

Griffiths, W.B., and Thomson, D.H. 2002. Species composition, biomass, and local distribution of zooplankton relative to water masses in the eastern Alaskan Beaufort Sea. In: Richardson, W.J., and Thomson, D.H., eds. Bowhead whale feeding in the eastern Alaskan Beaufort Sea: Update of scientific and traditional information, Vol. 1. OCS Study MMS 2002-12; LGL Report TA2196-7. Report from LGL Ltd., King City, Ontario, for U.S. Minerals Management Service, Anchorage, Alaska, and Herndon, Virginia. 5-1–5-42.

Harwood, L.A., Quakenbush, L.T., Small, R.J., George, J.C., Pokiak, J., Pokiak, C., Heide-Jørgensen, M.P., Lea, E.V., and Brower, H. 2017. Movements and inferred foraging by bowhead whales in the Canadian Beaufort Sea during August and September, 2006–12. Arctic 70(2):161–176.
https://doi.org/10.14430/arctic4648

Hauser, D.D.W., Laidre, K.L., Parker-Stetter, S.L., Horne, J.K., Suydam, R.S., and Richard, P.R. 2015. Regional diving behavior of Pacific Arctic beluga whales *Delphinapterus leucas* and possible associations with prey. Marine Ecology Progress Series 541:245–264.
https://doi.org/10.3354/meps11530

Hoekstra, P.F., Dehn, L.A., George, J.C., Solomon, K.R., Muir, D.C.G., and O'Hara, T.M. 2002. Trophic ecology of bowhead whales (*Balaena mysticetus*) compared with that of other Arctic marine biota as interpreted from carbon-, nitrogen-, and sulfur-isotope signatures. Canadian Journal of Zoology 80(2):223–231.
https://doi.org/10.1139/z01-229

Jonsen, I. 2016. Joint estimation over multiple individuals improves behavioural state inference from animal movement data. Scientific Reports 6: 20625.
https://doi.org/10.1038/srep20625

Jonsen, I.D., Flemming, J.M., and Myers, R.A. 2005. Robust state-space modeling of animal movement data. Ecology 86(11):2874–2880.
https://doi.org/10.1890/04-1852

Jonsen, I.D., Basson, M., Bestley, S., Bravington, M.V., Patterson, T.A., Pedersen, M.W., Thomson, R., Thygesen, U.H., and Wotherspoon, S.J. 2013. State-space models for bio-loggers: A methodological road map. Deep Sea Research Part II: Topical Studies in Oceanography 88-89:34–46.
https://doi.org/10.1016/j.dsr2.2012.07.008

Lee, S.H., Schell, D.M., McDonald, T.L., and Richardson, W.J. 2005. Regional and seasonal feeding by bowhead whales *Balaena mysticetus* as indicated by stable isotope ratios. Marine Ecology Progress Series 285:271–287.
http://doi.org/10.3354/meps285271

Lowry, L.F. 1993. Foods and feeding ecology. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. Special Publication 2. Lawrence, Kansas: The Society for Marine Mammalogy. 201–238.

Lowry, L.F., and Burns, J.J. 1980. Foods utilized by bowhead whales near Barter Island, Alaska, autumn 1979. Marine Fisheries Review 42(9-10):88–91.

Lowry, L.F., and Frost, K.J. 1984. Foods and feeding of bowhead whales in western and northern Alaska. Scientific Reports of the Whales Research Institute 35:1–16.

Lowry, L.F., Sheffield, G., and George, J.C. 2004. Bowhead whale feeding in the Alaskan Beaufort Sea based on stomach content analyses. Journal of Cetacean Research and Management 6(3):215–223.

Mate, B.R., Krutzikowsky, G.K., and Winsor, M.H. 2000. Satellite-monitored movements of radio-tagged bowhead whales in the Beaufort and Chukchi Seas during the late-summer feeding season and fall migration. Canadian Journal of Zoology 78(7):1168–1181.
https://doi.org/10.1139/z00-045

Melnikov, V.V., and Zeh, J.E. 2007. Chukotka Peninsula counts and estimates of the number of migrating bowhead whales. Journal of Cetacean Research Management 9(1):29–35.

Mocklin, J.A., Rugh, D.J., Moore, S.E., and Angliss, R.P. 2012. Using aerial photography to investigate evidence of feeding by bowhead whales. Marine Mammal Science 28(3):602–619.
https://doi.org/10.1111/j.1748-7692.2011.00518.x

Moore, S.E., and Reeves, R.R. 1993. Distribution and movement. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. Special Publication 2. Lawrence, Kansas: The Society for Marine Mammalogy. 313–386.

Natural Resource Council. 2003. Cumulative environmental effects of oil and gas activities on Alaska's North Slope. Washington, D.C.: The National Academies Press.

Niebauer, H.J., and Schell, D.M. 1993. Physical environment of the Bering Sea population. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. Special Publication 2. Lawrence, Kansas: The Society for Marine Mammalogy. 23–43.

Okkonen, S.R., Clarke, J.T., and Potter, R.A. 2018. Relationships among high river discharges, upwelling events, and bowhead whale (*Balaena mysticetus*) occurrences in the central Alaskan Beaufort Sea. Deep Sea Research Part II: Topical Studies in Oceanography 152:195–202.
https://doi.org/10.1016/j.dsr2.2016.11.015

Pickart, R.S. 2004. Shelfbreak circulation in the Alaskan Beaufort Sea: Mean structure and variability. Journal of Geophysical Research 109: C04024.
https://doi.org/10.1029/2003JC001912

Pomerleau, C., Matthews, C.J.D., Gobeil, C., Stern, G.A., Ferguson, S.H., and Macdonald, R.W. 2018. Mercury and stable isotope cycles in baleen plates are consistent with year-round feeding in two bowhead whale (*Balaena mysticetus*) populations. Polar Biology 41:1881–1893.
https://doi.org/10.1007/s00300-018-2329-y

Quakenbush, L.T., Citta, J.J., George, J.C., Small, R.J., and Heide-Jørgensen, M.P. 2010. Fall and winter movements of bowhead whales (*Balaena mysticetus*) in the Chukchi Sea and within a potential petroleum development area. Arctic 63(3):289–307. https://doi.org/10.14430/arctic1493

R Core Team. 2018. R: A language and environment for statistical computing. Version 3.5.1. Vienna, Austria: R Foundation. www.r-project.org

Reeves, R.R., Ewins, P.J., Agbayani, S., Heide-Jørgensen, M.P., Kovacs, K.M., Lydersen, C., Suydam, R., et al. 2014. Distribution of endemic cetaceans in relation to hydrocarbon development and commercial shipping in a warming Arctic. Marine Policy 44:375–389. https://doi.org/10.1016/j.marpol.2013.10.005

Robertson, F.C., Koski, W.R., and Trites, A.W. 2016. Behavioral responses affect distribution analyses of bowhead whales in the vicinity of seismic operations. Marine Ecology Progress Series 549:243–262. https://doi.org/10.3354/meps11665

Rugh, D.J. 1990. Bowhead whales reidentified through aerial photography near Point Barrow, Alaska. Report of the International Whaling Commission, Special Issue 12:289–294.

Rugh, D.J. and Cubbage, J.C. 1980. Migration of bowhead whales past Cape Lisburne, Alaska. Marine Fisheries Review 42(9-10):46–51.

Smultea, M.A., Fertl, D., Rugh, D.J., and Bacon, C.E. 2012. Summary of systematic bowhead surveys conducted in the U.S. Beaufort and Chukchi Seas, 1975–2009. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-237. 48 p.

Stafford, K.M., Citta, J.J., Okkonen, S.R., and Suydam, R.S. 2016. Wind-dependent beluga whale dive behavior in Barrow Canyon, Alaska. Deep-Sea Research Part I: Oceanographic Research Papers 118:57–65. https://doi.org/10.1016/j.dsr.2016.10.006

Stoker, S.W., and Krupnik, I.I. 1993. Subsistence whaling. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. Special Publication 2. Lawrence, Kansas: The Society for Marine Mammalogy. 579–629.

Thomson, D.H. 2002. Energetics of bowhead whales. In: Richardson, W.J., and Thomson, D.H., eds. Bowhead whale feeding in the eastern Alaskan Beaufort Sea: Update of scientific and traditional information, Vol. 1. OCS Study MMS 2002-12; LGL Report TA2196-7. Report from LGL Ltd., King City, Ontario, for U.S. Minerals Management Service, Anchorage, Alaska, and Herndon, Virginia. 22-1–22-40.

Walkusz, W., Williams, W.J., Harwood, L.A., Moore, S.E., Stewart, B.E., and Kwasniewski, S. 2012. Composition, biomass and energetic content of biota in the vicinity of feeding bowhead whales (*Balaena mysticetus*) in the Cape Bathurst upwelling region (south eastern Beaufort Sea). Deep-Sea Research Part I: Oceanographic Research Papers 69:25–35. https://doi.org/10.1016/j.dsr.2012.05.016

Wang, M., Yang, Q., Overland, J.E., and Stabeno, P. 2018. Sea-ice cover timing in the Pacific Arctic: The present and projections to mid-century by selected CMIP5 models. Deep-Sea Research Part II: Topical Studies in Oceanography 152:22–34. https://doi.org/10.1016/j.dsr2.2017.11.017

Williams, T.M. 2002. Swimming. In: Perrin, W.F., Würsig, B., and Thewissen, J.G.M., eds. Encyclopedia of marine mammals. San Diego: Academic Press. 1213–1222.

Wood, K.R., Overland, J.E., Salo, S.A., Bond, N.A., Williams, W.J., and Dong, X. 2013. Is there a "new normal" climate in the Beaufort Sea? Polar Research 32: 19552. https://doi.org/10.3402/polar.v32i0.19552

Würsig, B., and Clark, C.W. 1993. Behaviour. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. Special Publication 2. Lawrence, Kansas: The Society for Marine Mammalogy. 157–199.

Würsig, B., Koski, W.R., Thomas, T.A., and Richardson, W.J. 2002. Activities and behavior of bowhead whales in the eastern Alaskan Beaufort Sea during late summer and autumn. In: Richardson, W.J., and Thomson, D.H., eds. Bowhead whale feeding in the eastern Alaskan Beaufort Sea: Update of scientific and traditional information, Vol. 1. OCS Study MMS 2002-12; LGL Report TA2196-7. Report from LGL Ltd., King City, Ontario, for U.S. Minerals Management Service, Anchorage, Alaska, and Herndon, Virginia. 12-1–12-38.

Zeh, J.E., Clark, C.W., George, J.C., Withrow, D., Carroll, G.M., and Koski, W.R. 1993. Current population size and dynamics. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. Special Publication 2. Lawrence, Kansas: The Society for Marine Mammalogy. 409–489.