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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

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ABSTRACT. We analyzed data from line-transect aerial surveys for marine mammals conducted in the western Beaufort Sea (shore to 72˚ N, 140˚ – 157˚ W) from July to October of 2009 – 16 to investigate the distribution, behaviors, sighting rates, and habitat use preferences of bowhead and beluga whales. The habitat use data allowed for direct comparison with data collected in the same area from 1982 to 1991. Both species are ice-adapted, migrating through leads in sea ice in spring, and are seasonal inhabitants of the western Beaufort Sea during summer and fall. From 2009 to 2016, bowhead whales were seen in all survey months, with the highest overall sighting rate (whales per km) in August. Bowhead sighting rates were highest in the whales' preferred habitats: outer shelf habitat (51 – 200 m depth) in July and inner shelf-shallow habitat (≤ 20 m depth) in August, September, and October. Beluga whales were also seen in all survey months, with highest overall sighting rate in July. Beluga whales were overwhelmingly associated with continental slope habitat (201 – 2000 m depth) in all months. Bowhead whale distribution and depth preferences in summer months of 2009 – 16 differed from those observed in 1982 – 91, when bowheads were not seen during limited survey effort in July and preferred outer continental shelf habitat in August. These differences indicate that bowhead whale preference for shallow shelf habitat now occurs earlier in summer than it used to. Beluga whale distribution and depth preference remained similar between 1982 – 91 and 2009 – 16, with strong preference for continental slope during both periods. Differences in sea ice cover habitat association for both species are likely due more to the relative lack of sea ice in recent years compared to the earlier period than to shifts in habitat preference. Habitat partitioning between bowhead and beluga whales in the western Beaufort Sea remained evident except in July, when both species used continental slope habitat. In July – October 2009 – 16, the distribution, sighting rates, and behavior of both bowheads and belugas in the western Beaufort showed considerable interannual variation, which underscores the importance of annual sampling to accurate records of the complex western Beaufort Sea ecosystem.

Key words: bowhead whale; *Balaena mysticetus*; beluga whale; *Delphinapterus leucas*; Arctic; Beaufort Sea; habitat; aerial survey; feeding

RÉSUMÉ. Nous avons analysé les données découlant de levés aériens de transects linéaires pour mammifères marins, levés effectués dans l'ouest de la mer de Beaufort (de la rive jusqu'à 72˚ N, et de 140˚ jusqu'à 157˚ O) de juillet à octobre 2009 à 2016. Ces levés avaient pour but d'étudier la distribution, les comportements, les taux d'observation ainsi que les préférences d'utilisation de l'habitat des baleines boréales et des bélugas. Les données relatives à l'utilisation de l'habitat ont permis d'établir des comparaisons directes avec les données recueillies dans le même secteur de 1982 à 1991. Ces deux espèces sont adaptées à la glace, migrent par des chenaux formés dans la glace de mer au printemps et sont des habitants saisonniers de l'ouest de la mer de Beaufort pendant l'été et l'automne. Entre 2009 et 2016, des baleines boréales ont été aperçues pendant tous les mois visés par les levés, le taux d'observation général le plus élevé (nombre de baleines par km) ayant été enregistré au mois d'août. Les taux d'observation des baleines boréales étaient les plus élevés dans les habitats préférés de ces baleines, soit l'habitat de la plateforme externe (de 51 m à 200 m de profondeur) en juillet et l'habitat de la plateforme interne peu profonde (≤ 20 m de profondeur) en août, en septembre et en octobre. Des bélugas ont également été aperçus pendant tous les mois visés par les levés, le taux d'observation général le plus élevé ayant été enregistré en juillet. Les bélugas étaient massivement associés à l'habitat de la pente continentale (de 201 m à 2 000 m de profondeur) pendant tous les mois. La distribution et les préférences de profondeur des baleines boréales pendant les mois d'été 2009 à 2016 différaient de celles observées de 1982 à 1991, lorsque les baleines boréales n'ont pas été aperçues dans le cadre des quelques levés qui ont été effectués en juillet et préféraient leur habitat de la plateforme continentale externe en août. Ces différences indiquent que la préférence des baleines boréales pour l'habitat de la plateforme peu profonde se manifeste maintenant plus tôt l'été qu'auparavant. De 1982 à 1991 et de 2009 à 2016, la distribution des bélugas et leur préférence de profondeur sont restées semblables, avec une préférence marquée pour la pente continentale pendant les deux périodes. Pour les deux espèces, les différences sur le plan

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de l'association de la couverture de glace marine sont vraisemblablement davantage attribuables au manque relatif de glace de mer ces dernières années comparativement à la période précédente plutôt qu'à une variation de la préférence de l'habitat. Dans l'ouest de la mer de Beaufort, la séparation de l'habitat entre les baleines boréales et les bélugas demeurait évidente, sauf en juillet, quand les deux espèces utilisaient l'habitat de la pente continentale. De juillet à octobre 2009 à 2016, la distribution, les taux d'observation et le comportement des baleines boréales et des bélugas dans l'ouest de la mer de Beaufort ont affiché une variation considérable d'une année à l'autre, ce qui fait ressortir l'importance de faire des échantillonnages annuels afin d'obtenir des données précises au sujet de l'écosystème complexe de l'ouest de la mer de Beaufort.

Mots clés : baleine boréale; *Balaena mysticetus*; béluga; *Delphinapterus leucas*; Arctique; mer de Beaufort; habitat; levé aérien; alimentation

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INTRODUCTION

Widespread ecosystem changes, including dramatic decreases in annual summer sea ice, increased duration of open water periods, and geographic and temporal variations in upwelling-favorable conditions, have altered the seasonal habitat encountered by cetaceans in the Pacific Arctic (Stroeve et al., 2007; Grebmeier, 2012; Walkusz et al., 2012; Wood et al., 2015). Two cetacean species, bowhead whales (*Balaena mysticetus*) and beluga whales (*Delphinapterus leucas*), occur regularly in the Beaufort Sea from mid-spring through early fall, migrating to the region to feed in areas that overlap with offshore oil and gas development.

Bowhead whales are ice-adapted baleen whales, capable of breaking through sea ice at least 18 cm thick (George et al., 1989). Bowheads of the Bering-Chukchi-Beaufort (BCB) stock typically migrate each spring from wintering grounds in the western Bering Sea through leads in the sea ice in the eastern Chukchi and western Beaufort Seas en route to their summer habitat in the eastern Beaufort Sea (Moore and Reeves, 1993; Quakenbush et al., 2013). Most of the BCB stock takes advantage of aggregations of copepods and euphausiids that occur along areas of upwelling near Cape Bathurst and Tuktoyaktuk Peninsula in the eastern Beaufort Sea during the open water season each year (Walkusz et al., 2012; Citta et al., 2015). During the summer months, some bowheads also remain in the Chukchi Sea (Melnikov and Zeh, 2007; Quakenbush et al., 2010), travel to Canadian High Arctic waters (Heide-Jørgensen et al., 2012; Quakenbush et al., 2013), or traverse the Beaufort Sea multiple times (Christman et al., 2013; Quakenbush et al., 2013). Aerial survey, telemetry, and passive acoustic monitoring results available to date have shown that during the open water season, bowheads tend to use western Beaufort shelf habitat shallower than 200 m (Moore et al., 2000; Blackwell et al., 2007; Clark et al., 2015; Clarke et al., 2017). In some parts of their range, they exhibit considerable individual variation, including age and sex segregation (Koski et al., 1988; Koski and Miller, 2002; Harwood et al., 2017), and they make multiple stops lasting days or weeks at feeding locations offshore of the Alaska North Slope, probably after they have already spent days to months feeding in the eastern Beaufort Sea (Citta et al., 2015; Kuletz et al., 2015; Harwood et al., 2017). The bowheads' westward migration from the eastern Beaufort Sea to the northeastern Chukchi Sea is protracted, occurring from July through at least early November (Citta et al., 2015; Lin et al., 2016).

Beluga whales are ice-associated toothed whales found in Arctic and subarctic habitats. Two stocks, the Eastern Chukchi Sea (ECS) stock and the Eastern Beaufort Sea (EBS) stock, are found in the Beaufort Sea in mid-spring, summer, and fall. Both stocks migrate each spring from wintering grounds in the Bering Sea (Citta et al., 2017), but migration occurs independently for each stock, and each uses unique areas for calving and molting in early summer (Richard et al., 2001; Suydam et al., 2001). Belugas disperse from coastal molting areas to the deeper waters of the Beaufort Sea (Stafford et al., 2013, 2017; Garland et al., 2015), where distribution is temporally and geographically stratified, and overlap between stocks is limited mainly to September (Hauser et al., 2014). Distribution is likely closely related to prey availability. Belugas feed on fishes, including Arctic cod (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*), and a wide array of invertebrates and cephalopods (Seaman et al., 1982; Quakenbush et al., 2015). Belugas move westward from July through October, crossing the Beaufort Sea but traveling seaward of the 200 m isobath (Moore et al., 2000; Richard et al., 2001).

From 1982 to 1991, broad-scale aerial surveys were conducted annually in the western Beaufort Sea from July to October (Moore, 2000; Moore et al., 2000). From 1992 to 2010, surveys in the western Beaufort Sea were conducted mainly in September and October (e.g., Monnett and Treacy, 2005; Clarke et al., 2011), primarily to monitor the bowhead whale migration. Under the auspices of the Aerial Surveys of Arctic Marine Mammals (ASAMM) project, the survey period in the western Beaufort Sea was extended to mid-August in 2011 and to mid-July from 2012 to 2016. The ASAMM project, funded by the Bureau of Ocean Energy Management and its precursor, the Minerals Management Service, was initially designed to examine the potential effects of petroleum exploration and development on bowheads in nearshore areas of the western Beaufort Sea. While that objective remains an important part of the study, ASAMM also documents the distribution and relative abundance of all marine mammals, monitors areas of importance for behaviors such as calving, pupping, feeding,

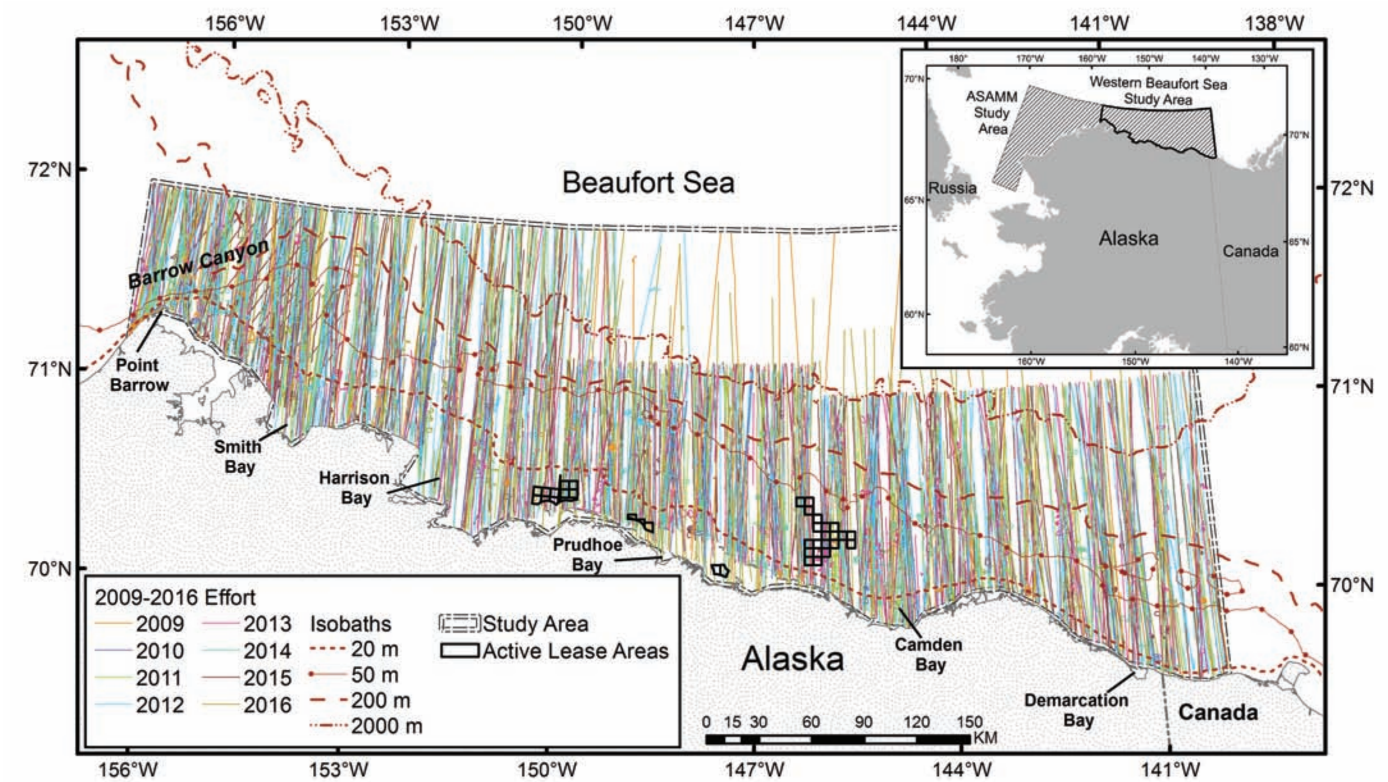

FIG. 1. Western Beaufort Sea study area and survey effort (transect plus circling-on-transect kilometers), 2009 – 16. Inset shows the western Beaufort Sea study area (outlined in black) relative to the entire ASAMM study area (diagonal stripes).

hauling out, and migrating, and provides a dataset that can be used to compare cetacean habitat use over a span of more than 30 years.

In the 1980s, Moore et al. (2000) used aerial survey data from the western Beaufort Sea to establish that bowhead whales there were associated with moderate ice conditions and 51 – 2000 m depths in summer and light ice conditions and depths of less than 50 m in fall, while beluga whales were associated with moderate to heavy ice and depths greater than 200 m in summer and moderate to heavy ice and 51 – 2000 m depths in fall. Here, we augment the data described in Moore et al. (2000) with an additional eight years (2009 – 16) of data from recent aerial surveys. We seek to examine broad patterns and variability in the distribution of both whale species, between and within time periods, and examine relationships of distribution and variability patterns to water depth and sea ice. Although ASAMM surveys extend into the eastern Chukchi Sea, this paper is limited to the western Beaufort Sea to focus on areas where the distributions of bowhead and beluga whales overlap from July through October. Gray whales, included in Moore et al. (2000), were not included here because of the paucity of sightings in the Beaufort Sea. Bowhead and gray whale distributions, sighting rates, and habitat preferences in the eastern Chukchi Sea in 1982 – 91 and 2009 – 15 are compared in Clarke et al. (2016).

METHODS

Surveys and Analysis, 2009 – 16

The study area in the western Beaufort Sea extends from shore to 72˚ N and from 140˚ W to 157˚ W. This area totals 111 700 km^2, comprises the eastern portion of the ASAMM survey area (Fig. 1) and overlies all of the active petroleum leases in the Alaskan Beaufort Sea. Data collected within this study area provide the best comparison between recent (2009 – 16) and historical (1982 – 91) data on bowhead and beluga whales because this area generally coincides with the Beaufort Sea study area of Moore et al. (2000), although the latter extended north to 73˚ N between 154˚ W and 157˚ W, outside of the current ASAMM study area. Surveys were flown from mid-July to late October in Turbo Commander (2009 – 16) and de Havilland Twin Otter™ (2009 – 10) aircraft. All survey aircraft were outfitted with bubble windows, which allow detection of marine mammals directly under the aircraft. Line-transect aerial surveys were flown at 305 to 460 m altitude, maintaining a survey speed of approximately 220 km/h. Transects were oriented perpendicular to shore in order to sample across isobaths, prevailing currents, and expected gradients in marine mammal density. Transects were spaced at intervals of one-half degree of longitude and were derived independently for each survey so that unique areas were surveyed during every flight. The selection of transects to be flown on a given day was not random; it was based on reported or observed weather conditions in the study area, avoidance of recently surveyed areas, and the need to deconflict with other aerial operations or marine subsistence users. In general, surveys were planned to distribute effort fairly evenly across the survey area.

The survey protocols described here for 2009–16 were similar to those used in the historical surveys conducted from 1982 to 1991 (although see Clarke et al., 2016 for exceptions). Two primary observers, one on each side of the aircraft, maintained a continuous watch for marine mammals while a third observer/data recorder entered data into a laptop computer for each sighting, whenever survey conditions changed, or every five minutes. Sightings made by primary observers on transect were considered on-effort sightings because primary observers were always actively searching, while sightings made by non-primary observers (e.g., data recorder, pilots) were considered off-effort. Systematic transect coverage included all depth and sea ice habitats without bias toward or against areas with the highest likelihood of sightings. The aircraft made brief (< 10 min) diversions from transects to circle large whale groups to identify whales to species, estimate group size, and search for calves. A continuously updated map display on the onboard laptop computer minimized the chances that duplicate sightings would be recorded during circling or after returning to transect. Transits between targeted survey areas or transects, or survey effort along transect lines when weather was too poor for visual observations, were recorded as off-effort. Off-effort sightings and kilometers were not included in any analyses. The ASAMM database does not specifically identify effort and sightings during circling-on-transect events prior to 2009, so those data were not included in this analysis.

Data routinely logged when whales were seen included time, altitude, latitude, longitude, sea state, sea ice type and percent cover, visibility conditions, declination angle from the horizon to the sighting to determine the whales' distance from the transect line (not recorded during circling), species, number of whales, number of calves, sighting cue, whales' behavior, and initial heading. Locations of whales observed during circling events were recorded as the position of the aircraft as it flew overhead. Behavioral classifications included swim, dive, feed, mill, rest, and several types of displays. Feeding was inferred when bowhead whales were observed with mud on the rostrum or streaming from the mouth, exhibiting synchronous diving and surfacing, swimming in echelon formation at the surface, or swimming at or near the surface with mouth open. Sea state was classified according to the Beaufort wind force scale (Maloney, 2006), and sea ice cover was estimated as the percentage of the sea surface visible to observers that was ice covered. Additional survey protocol details are provided elsewhere (e.g., Clarke et al., 2017).

Sighting rates can be considered a measure of relative density because they were not corrected for availability or perception bias (Buckland et al., 2001); absolute density was not calculated because track line detection probability for these surveys is unknown. Sighting rates were calculated for each depth zone to compare the monthly and seasonal relative densities (whales per km) for both bowhead and beluga whales (summer is July and August; fall is September and October). Sighting rates were computed in two ways. First, to best convey patterns in relative density similar to those presented in Clarke et al. (2016), both transect and circling-on-transect kilometers and whales were used to calculate 2009–16 sighting rates for each depth zone. Second, for consistency with the remaining analyses presented in this paper, sighting rates per depth zone were calculated using whales and effort limited to sightings on transect only. All on-effort sightings from primary observers, regardless of environmental conditions, were used in analyses. Data were not collected when Beaufort wind force was greater than five, visibility conditions were poor, or survey altitude was less than 305 m. Total distance per depth zone was calculated by clipping the transect lines to polygons defined by isobaths, using ESRI ArcGIS version 10.1.

Depth zones generally followed Moore et al. (2000) except for the inner shelf region, and correspond to broad patterns of Pacific water masses in the Beaufort Sea (Aagaard, 1984). Five depth zones were identified:

- Inner shelf-shallow (14% of study area) is 20 m or less deep, encompassing wind-driven surface currents and greater influence from freshwater river runoff;
- Inner shelf-deep (20% of study area) is 21–50 m deep, encompassing wind-driven currents and less influence from freshwater river runoff;
- Outer shelf (15% of study area) is 51–200 m depth, encompassing the Beaufort Undercurrent and the Beaufort shelfbreak jet (Nikolopoulos et al., 2009);
- Continental slope (18% of study area) is 201–2000 m depth, also encompassing the Beaufort Undercurrent;
- Basin (33% of study area) is more than 2000 m deep, encompassing the Beaufort Gyre.

Depth zone boundaries were digitally derived and based on depth data in the International Bathymetric Chart of the Arctic Ocean (IBCAO) Version 2.23 (Jakobsson et al., 2008), which had a pixel resolution of 2 km.

To determine whether the distribution of whales was uniform in each month and season with respect to depth, permutation tests (Legendre and Legendre, 1998) using the chi-squared test statistic, χ^2, were used:

$$\chi^2 = \sum_i \frac{(A_i - E_i)^2}{E_i}$$

A_i and E_i respectively are the actual and expected number of whales observed on transect per depth zone category *i*. Under the null hypothesis that whales were distributed uniformly throughout the study area, the expected number of whales is directly proportional to transect survey effort. Therefore, E_i was computed as the total number of whales observed on transect in the study area multiplied by the proportion of transect effort in stratum *i*. Because individual whales observed in groups and recorded in a single sighting were not independent of each other, the standard chi-squared distribution could not be used to determine whether the test statistic was valid. Instead, we generated a sampling distribution by randomly permuting the depth zones in each monthly or seasonal data subset for each species 500 000 times and computing χ^2 for each permutation. For each analysis, the significance of the actual χ^2 test statistic computed from the observed data was assessed in comparison to the distribution of the 500 000 χ^2 values derived from the random permutations.

Calculation of habitat selection ratios followed Moore et al. (2000). Habitat selection ratios (w_i) provide indices of habitat use comparable between species and seasons (see Moore et al., 2000; Manly et al., 2002). These ratios were calculated as:

$$w_i = o_i/\pi_i$$

where, o_i = proportion of whales observed on transect in depth zone *i*; and π_i = proportion of effort (km on transect) in depth zone *i* (π_i was identified as pE_i in Moore et al., 2000). If $w_i > 1$, the proportion of whales in depth zone *i* is greater than expected if distribution were uniform, given the proportion of effort in depth zone *i*. If $w_i < 1$, the proportion of whales in depth zone *i* is less than expected if distribution were uniform, given the proportion of effort in depth zone *i*. The probability that a randomly selected whale would be in depth zone *i* if there were equal survey effort across all depth zones could be computed by standardizing the selection ratios, assuming that individual whales were independently distributed. However, feeding whales tend to be aggregated into groups, and cow-calf pairs are found in close association with each other, so the assumption of independence does not hold. Therefore, we did not compute standardized habitat selection ratios. Habitat selection implies that whales are actively selecting certain habitats. Because track line detection probability is not currently known for these surveys, habitat selection ratios presented here are more representative of habitat use.

Depth and Sea Ice Habitat Use, 1982–91 vs. 2009–16

To compare habitat use by bowhead and beluga whales observed in the western Beaufort Sea in 1982–91 with that observed in 2009–16, we used a data subset that was selected to ensure that as many variables as possible were equivalent between the two periods. Direct comparison of bowhead and beluga sighting rates from the periods 1982–91 and 2009–16 is not possible because of the different survey platforms and data collection protocols, which likely affect detection probabilities, as discussed in Clarke et al. (2016). However, chi-squared permutation tests were used to determine whether the distribution of whales was uniform with respect to depth or sea ice concentration in each month and season. We also investigated whether the bowhead and beluga whale sightings on transect (without reference to group size) during each period were distributed uniformly across depth zones using the chisq.fun function in R. For this analysis, the expected number of sightings per depth zone was computed as the total number of sightings on transect in the study area multiplied by the proportion of transect effort in that zone. Habitat selection ratios using whales and effort on transect in 1982–91 and 2009–16 allow us to determine habitat preferences within each time period and to compare the two time periods. Data from 1982–91 were reanalyzed using number of whales rather than number of sightings to better incorporate multi-animal groups, including cow-calf pairs and feeding groups. Geographic, temporal, and depth zone parameters remained the same as described above. Depth zones were based on the same digitally derived boundaries described above, except that the inner shelf depth zone included ≤ 50 m depths to align with Moore et al. (2000). Total distance per depth zone was calculated using the method described above. Sea ice habitat selection used the same sea ice categories as Moore et al. (2000): 0%–10%, open water/light; 11%–40%, light/moderate; 41%–70%, moderate/heavy; 71%–100%, heavy. For each sea ice category, we calculated total distance (transect kilometers) by summing the distances from all transects using ESRI ArcGIS version 10.4. The 1982–91 Beaufort Sea data do not distinguish primary observers from other observers; therefore, to compare habitat use between that period and 2009–16, we used data from all observers to determine the number of whales sighted in each period.

RESULTS

Survey Effort, Sighting Distribution, and Sighting Rates, 2009–16

More than 167 000 km (transect and circling-on-transect) were flown in the western Beaufort Sea from 2009 to 2016 (Fig. 1), with variation among years and months (Table 1, Fig. 2). Surveys were concentrated on the Beaufort Sea shelf and slope because those areas overlapped offshore oil and gas exploration and production areas. Effort in the northeastern part of the study area was largely limited to 2016, when surveys were extended into deeper water areas to target beluga habitat specifically. Annual survey effort was greatest in 2016 (> 34 000 km) (Fig. 2). Monthly effort across all years was highest in September (> 64 000 km total; mean of 8083 km per year) and lowest in July (< 24 000 km; mean of 2909 km per year). Surveys were regularly conducted in July and August from 2012 to 2016; only 3% of total summer effort occurred in 2009–11. Half (50%) of total effort was in the inner shelf (0–50 m) depth zone, while only 7% of total effort was in the basin (> 2000 m) depth zone (Table 1, Fig. 1).

TABLE 1. Sightings of bowhead and beluga whales in the western Beaufort Sea study area, 2009–16. Survey effort (km) includes kilometers flown on transect plus circling-on-transect. S (W) indicates number of sightings and (in parentheses) number of whales sighted. Sighting rate (SR), or number of whales per kilometer, is given for each depth zone in each month and season. Bold font indicates the maximum sighting rate for each month and season.

	July			August			Summer		
Bowhead whale:	km	S (W)	SR	km	S (W)	SR	km	S (W)	SR
Inner shelf-shallow (≤ 20 m)	3224	7 (12)	0.0037	7100	218 (804)	**0.1132**	10 324	225 (816)	**0.0790**
Inner shelf-deep (21–50 m)	7001	11 (15)	0.0021	15 308	368 (569)	0.0372	22 309	379 (584)	0.0262
Outer shelf (51–200 m)	5273	57 (103)	**0.0195**	10 804	188 (298)	0.0276	16 077	245 (401)	0.0249
Continental slope (201–2000 m)	5411	40 (64)	0.0118	9466	27 (45)	0.0048	14 877	67 (109)	0.0073
Basin (> 2000 m)	2364	2 (2)	0.0008	3851	3 (4)	0.0010	6215	5 (6)	0.0010
Total	23 273	117 (196)	0.0084	46 530	804 (1720)	0.0370	69 804	921 (1916)	0.0274
Beluga whale:									
Inner shelf-shallow (≤ 20 m)	3224	7 (11)	0.0034	7100	19 (36)	0.0051	10 324	26 (47)	0.0046
Inner shelf-deep (21–50 m)	7001	29 (87)	0.0124	15 308	40 (155)	0.0101	22 309	69 (242)	0.0108
Outer shelf (51–200 m)	5273	82 (369)	0.0700	10 804	95 (391)	0.0362	16 077	177 (760)	0.0473
Continental slope (201–2000 m)	5411	536 (1646)	**0.3042**	9466	638 (2770)	**0.2926**	14 877	1174 (4416)	**0.2968**
Basin (> 2000 m)	2364	92 (202)	0.0855	3851	109 (171)	0.0444	6215	201 (373)	0.0600
Total	23 273	746 (2315)	0.0995	46 530	901 (3523)	0.0757	69 804	1647 (5838)	0.0836

	September			October			Fall		
Bowhead whale:	km	S (W)	SR	km	S (W)	SR	km	S (W)	SR
Inner shelf-shallow (≤ 20 m)	11 371	381 (915)	**0.0805**	6448	156 (326)	**0.0506**	17 819	537 (1241)	**0.0696**
Inner shelf-deep (21–50 m)	22 337	525 (806)	0.0361	10 545	106 (184)	0.0174	32 882	631 (990)	0.0301
Outer shelf (51–200 m)	14 324	151 (201)	0.0140	8321	109 (171)	0.0206	22 644	260 (372)	0.0164
Continental slope (201–2000 m)	11 893	23 (30)	0.0025	6054	11 (18)	0.0030	17 947	34 (48)	0.0027
Basin (> 2000 m)	4502	0 (0)	0.0000	1557	0 (0)	0.0000	6058	0 (0)	0.0000
Total	64 427	1080 (1952)	0.0303	32 924	382 (699)	0.0212	97 352	1462 (2651)	0.0272
Beluga whale:									
Inner shelf-shallow (≤ 20 m)	11 371	26 (50)	0.0044	6448	6 (7)	0.0011	17 819	32 (57)	0.0032
Inner shelf-deep (21–50 m)	22 337	20 (31)	0.0014	10 545	11 (31)	0.0029	32 882	31 (62)	0.0019
Outer shelf (51–200 m)	14 324	84 (259)	0.0181	8321	93 (442)	0.0531	22 644	177 (701)	0.0310
Continental slope (201–2000 m)	11 893	353 (771)	**0.0648**	6054	226 (696)	**0.1150**	17 947	579 (1467)	**0.0817**
Basin (> 2000 m)	4502	42 (123)	0.0273	1557	3 (5)	0.0032	6058	45 (128)	0.0211
Total	64 427	525 (1234)	0.0192	32 924	339 (1181)	0.0359	97 352	864 (2415)	0.0248

There were 2383 on-effort sightings of 4567 bowhead whales in the western Beaufort Sea from 2009 to 2016 (Table 1). Bowheads were seen during all survey months, with the greatest number of sightings and total whales in September (Table 1, Fig. 3B). There were relatively few sightings in July, despite more than 23 000 km of effort. Sightings in July were distributed from 140˚ W to 149˚ W and 150.5˚ W to 156˚ W, with a gap in distribution near Harrison Bay (Fig. 3A), and most bowheads were seen offshore on the outer shelf or slope. In August, bowhead whales were distributed across the entire western Beaufort Sea with no gaps in distribution, and seen in all depth zones (Fig. 3A). Sightings were also broadly distributed throughout the study area in September and October, with more sightings on the inner shelf and near Barrow Canyon and fewer sightings on the slope or basin, when compared to summer (Fig. 3B). No bowhead whales were seen between barrier islands and the mainland, probably because the water is too shallow (although survey effort was also limited in those areas). Monthly sighting rates were lowest in July, quadrupled in August, and decreased in September and again in October (Table 1). The sighting rate was highest in the inner shelf-shallow (≤ 20 m) depth zone in both summer and fall (Table 1). The annual sighting rate ranged from a low of 0.0054 whales/km in 2011 to a

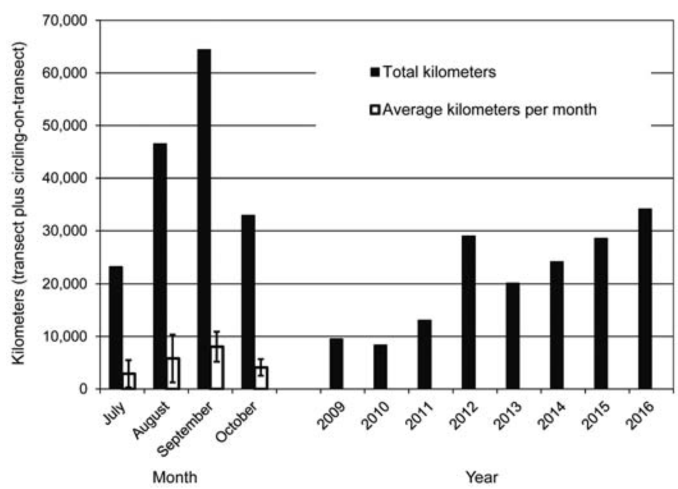

FIG. 2. Summary of monthly and annual kilometers (transect plus circling-on-transect kilometers) flown during aerial surveys of marine mammals in the western Beaufort Sea from July to October in 2009–16. Error bars represent one standard deviation of average kilometers per month.

high of 0.0476 whales/km in 2016. Fall sighting rates were higher than summer rates in all years except 2013 and 2016 (Fig. 4A); in 2016, the summer sighting rate was more than twice as high as the fall sighting rate. As expected, annual and seasonal sighting rates using effort and whales on

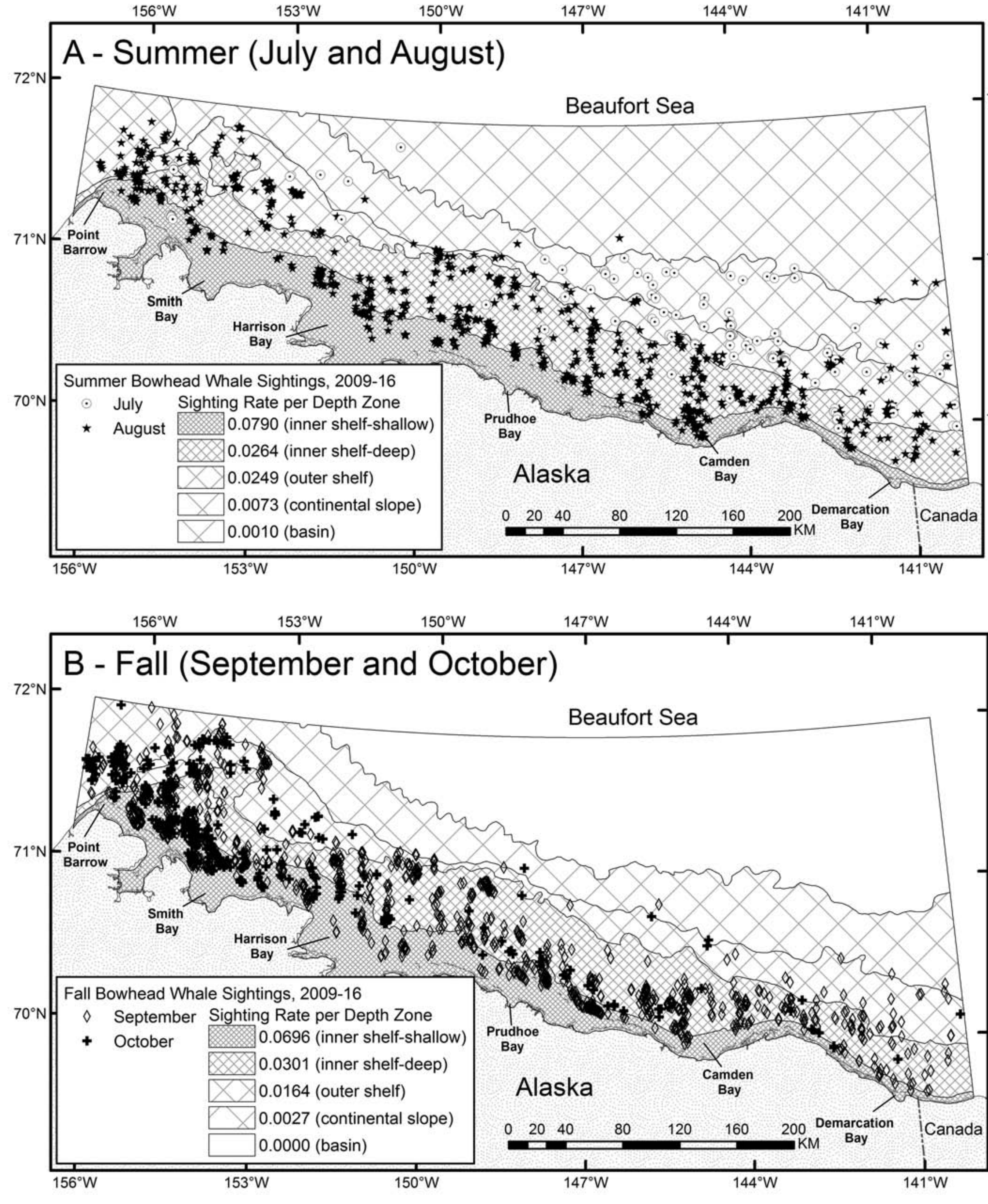

FIG. 3. Bowhead whale sightings per month and sighting rate (whales per km) for each depth zone in (A) summer (July and August) and (B) fall (September and October), 2009–16. Includes transect plus circling-on-transect sightings. Heavy shading represents highest sighting rate and no shading represents lowest sighting rate.

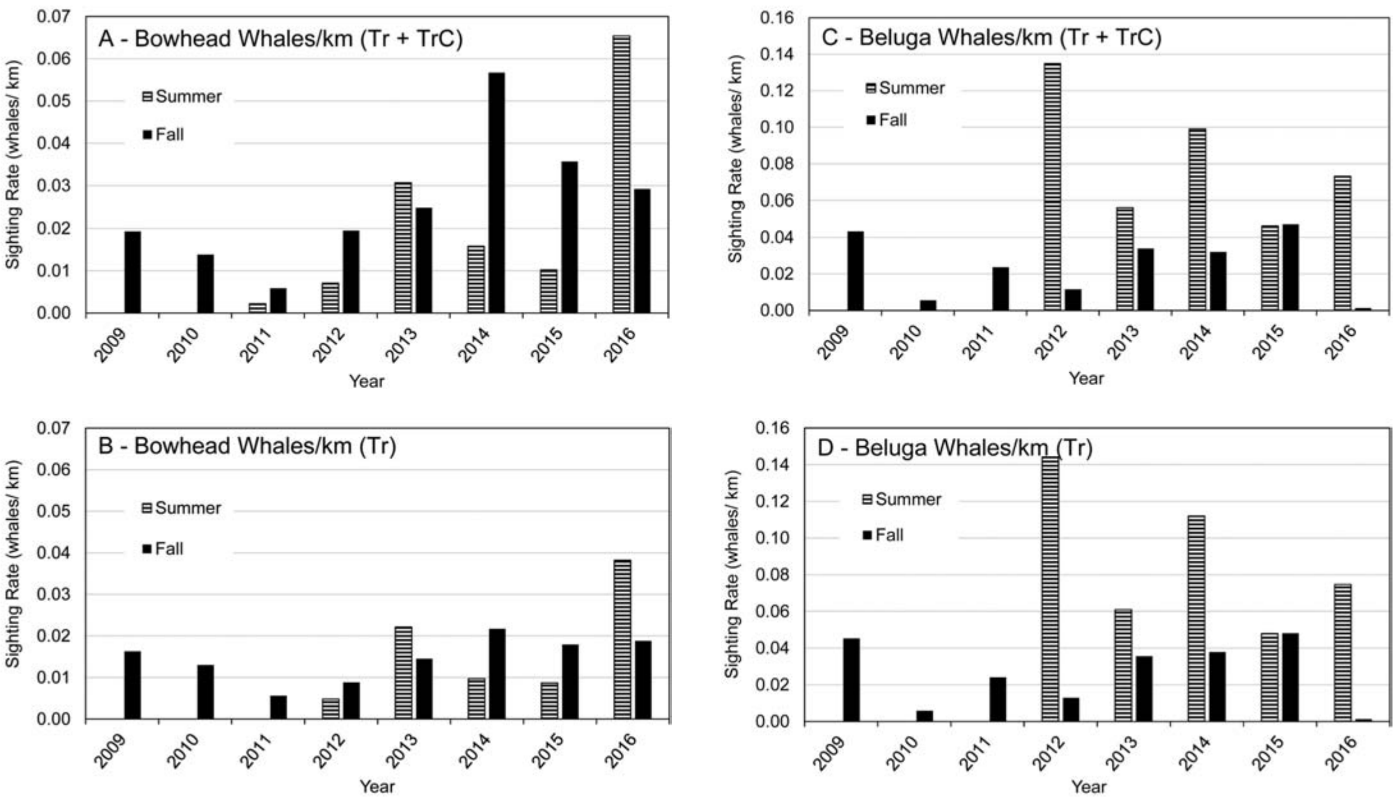

FIG. 4. Sighting rates (whales/km) for bowhead (A, B) and beluga (C, D) whales in the western Beaufort Sea in summer and fall of 2009–16. Tr = transect; Tr + TrC = transect plus circling-on-transect.

transect only were lower than those incorporating effort and whales on circling, but the overall trends remained the same (Fig. 4B).

Additional information about bowhead whales' use of the western Beaufort Sea was gleaned from the data on behavior and sea ice cover. Bowheads were mainly recorded as swimming (1906 whales, 42%) or feeding (1208 whales, 26%). Bowhead feeding behavior is likely underreported in aerial survey data because it is difficult to assess, particularly for whales feeding near the bottom or in the water column (Lowry, 1993; Lowry et al., 2004). Bowheads were recorded as milling when there was no direct evidence of feeding activity; in reality, however, milling whales (738 whales, 16%) may be foraging as well. Feeding was recorded in all months, with the highest proportion of feeding to all behaviors occurring in August (36%). Interannual variability was strong, with feeding rarely observed (138 whales) in 2009–10 and in 2012–13, and not observed at all in 2011 (Fig. 5). Feeding observations were temporally and geographically clumped in 2014, 2015, and 2016. In 2014, feeding was observed primarily in the central Alaskan Beaufort Sea from Camden Bay to north of Prudhoe Bay (~145˚ W to 148.5˚ W) from late August to early October. In 2015, feeding was observed primarily in the western Alaskan Beaufort Sea from just west of Harrison Bay to Point Barrow (~151.5˚ W to 157˚ W) from late August to early October. In 2016, feeding behavior was observed in three areas: Camden Bay in August, Harrison Bay from early August through early September, and Barrow Canyon in late August. Feeding was occasionally observed in areas where water depths exceeded 200 m, but most feeding (87%) was observed on the inner shelf where water depths were 20 m or less. Bowheads were seen in up to 80% broken floe sea ice, although most bowheads (92%) were seen in the ice-free conditions that were prevalent in late summer and fall in the study area. In most years, the sea ice edge was farther north than the extent of survey effort, particularly in fall.

For beluga whales, there were 2511 on-effort sightings of 8253 individuals in the western Beaufort Sea in 2009–16 (Table 1). Beluga whales were seen during all survey months (Fig. 6), with the greatest number of sightings and total whales in August (Table 1). Belugas were seen predominantly on the continental slope and basin in both summer and fall (Fig. 6). The lack of belugas in most of the northeastern part of the study area is likely due to the relative lack of survey effort in that region (see Fig. 1). Belugas were occasionally sighted in nearshore, inner shelf waters (< 50 m), but those observations accounted for only 5% of total belugas seen. The sighting rate was highest in July, decreased in August and again in September, and increased in October (Table 1). In four of the five years (2012–16) when surveys were regularly conducted during summer months, the sighting rate was noticeably higher in summer than in fall (Fig. 4C); in 2015, however, the fall sighting rate was slightly higher. The difference in seasonal

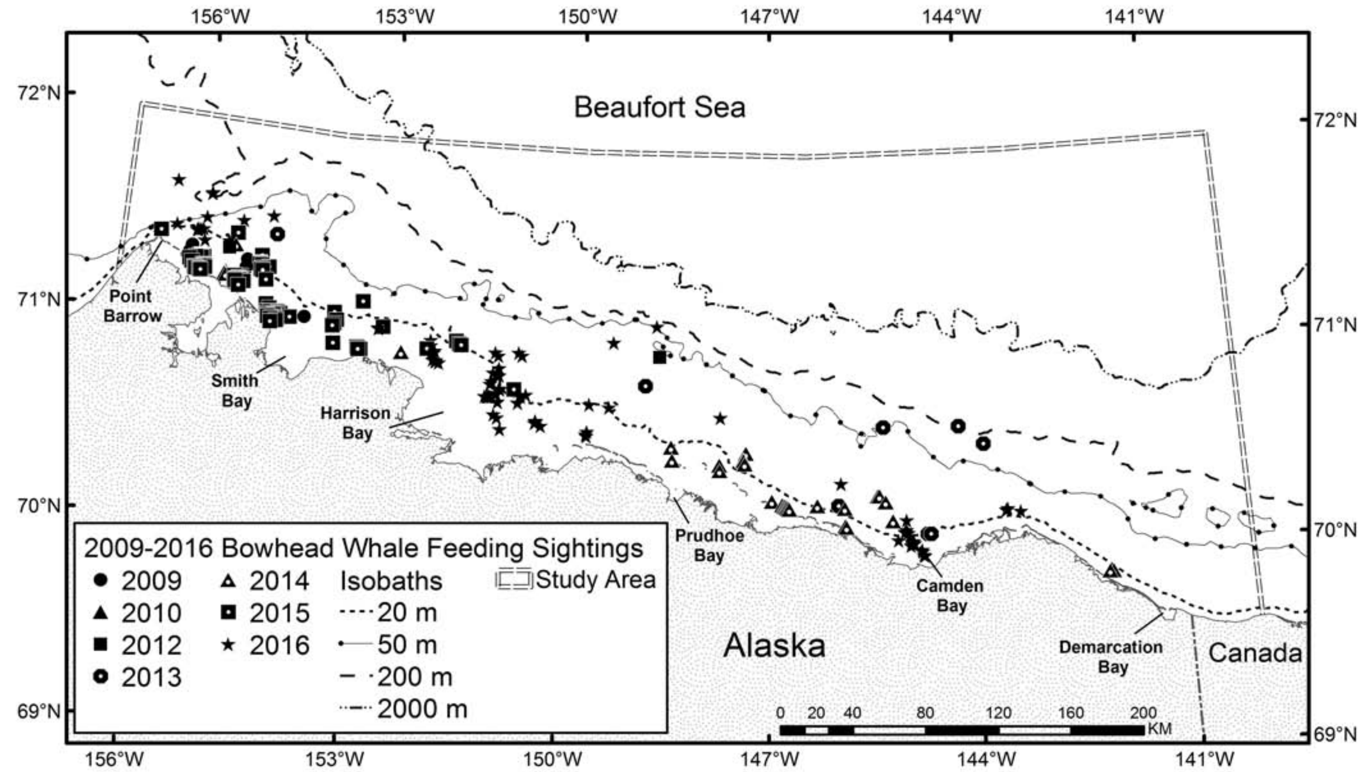

FIG. 5. Sightings of feeding bowhead whales (on transect plus circling-on-transect) in the western Beaufort Sea, 2009–16.

sighting rate was particularly striking in 2016, when the summer sighting rate was 56 times the fall sighting rate; only 21 belugas were seen during September and October 2016 (Clarke et al., 2017). Sighting rates using whales and effort on transect differed only slightly (Fig. 4D) from the sighting rate analysis that incorporated whales and effort on circling primarily because beluga sightings were rarely circled. The highest sighting rate was in continental slope (201–2000 m) depth zone in both summer and fall, while the lowest sighting rate was in the inner shelf-shallow in summer and the inner shelf-deep in fall (Table 1).

Most beluga whales were recorded as swimming (6407 whales, 78%) and were headed west, with the exception of belugas seen in the Barrow Canyon area in summer, which were headed east. Belugas were seen in up to 99% ice cover, although most whales (56%) were seen in the ice-free conditions that were present in late summer and throughout fall in the study area. Most (98%) of the belugas observed near sea ice were seen in July and August, when sea ice was still present in offshore areas with deeper water.

Seasonal Habitat Use, 2009–16

Results from permutation tests on summer depth distribution were significant for bowhead whales, but not for beluga whales (Table 2). In summer, bowheads preferred inner shelf-shallow habitat (≤ 20 m; $w_i = 2.797$), with minimal preference for continental slope or basin (> 201 m depth) habitat, while belugas overwhelmingly preferred continental slope (201–2000 m; $w_i = 3.336$), with minimal use of inner shelf-shallow waters (≤ 20 m; $w_i = 0.056$) (Table 2). Comparison of selection ratios of bowhead and beluga whales indicated that there was essentially no overlap in preferred habitat between the two species in summer. Bowheads were 50 times as likely as belugas to use inner shelf-shallow habitat, and belugas were 10 times as likely as bowheads to use continental slope. Bowheads showed some preference for inner shelf-deep and outer shelf habitat, whereas belugas rarely used those depth zones.

Permutation tests on fall depth distributions were not significant for bowheads or belugas when number of individuals was used (Table 2) but were significant for both species when number of sightings was used. Bowhead habitat selection ratios (w_i) showed that in fall, bowheads were more likely to be seen in inner shelf-shallow habitat (≤ 20 m; $w_i = 2.251$) and, to a lesser extent, in inner shelf-deep habitat (21–50 m; $w_i = 1.252$), than in any other depth zone (Table 2). Bowheads used inner shelf habitat (≤ 50 m) five times as frequently as outer shelf, slope, and basin habitat (> 50 m) (Table 2). Beluga habitat preference in fall remained overwhelmingly for continental slope habitat (201–2000 m; $w_i = 3.071$), and belugas were least likely to use inner shelf-deep habitat (21–50 m; $w_i = 0.080$). In fall, as in summer, habitat preferences of bowhead and beluga whales barely overlapped. Bowheads used inner shelf-shallow habitat nearly 17 times as often as belugas in fall, while belugas were 26 times as likely as bowheads to use continental slope habitat (Table 2).

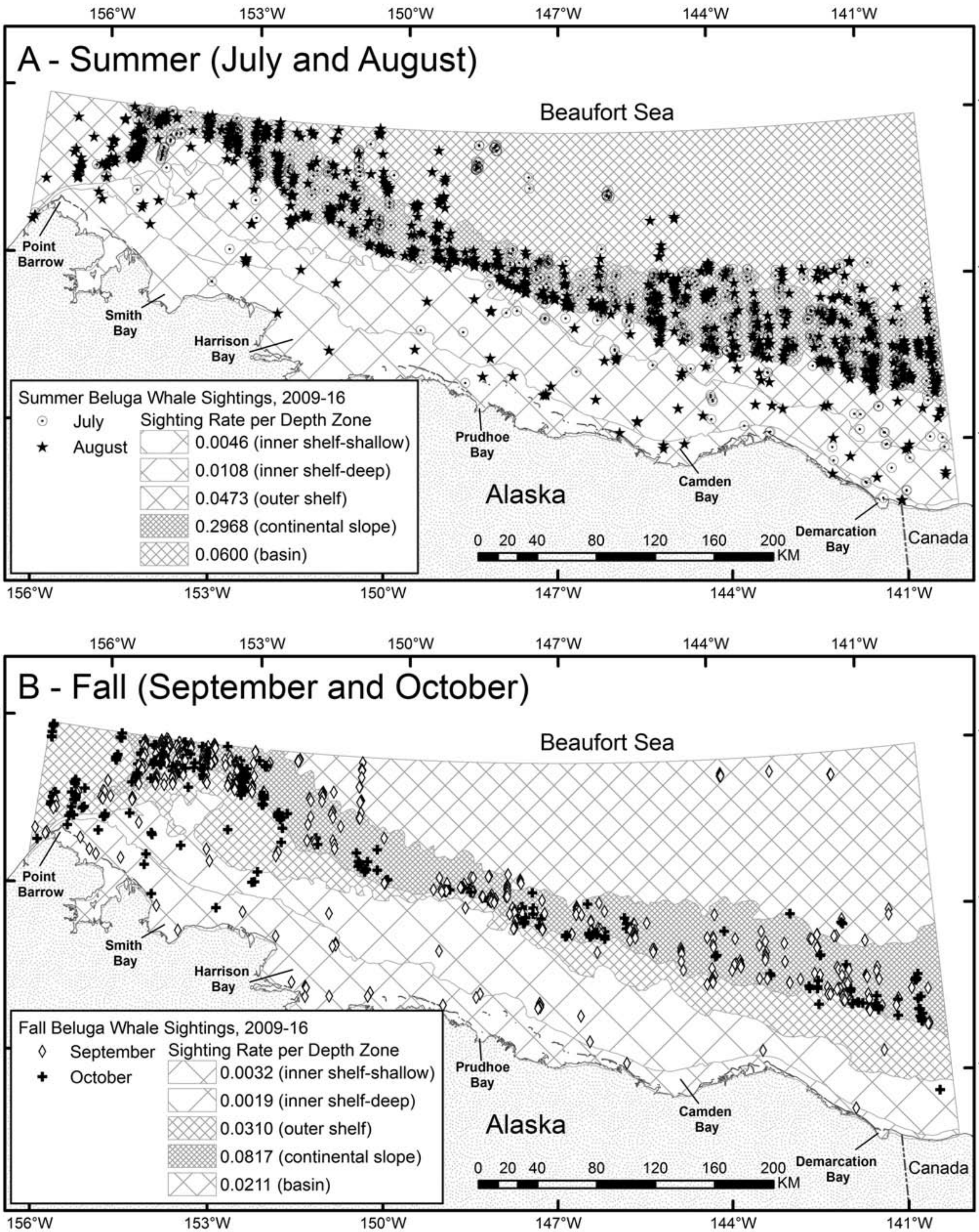

FIG. 6. Beluga whale sightings per month and sighting rate (whales per km) for each depth zone in (A) summer (July and August) and (B) fall (September and October), 2009–16. Details as in Figure 3.

TABLE 2. Seasonal summary by depth zone and depth selection ratios (w_i) of bowhead and beluga whales sighted on transect in the western Beaufort Sea, 2009–16. Tr km refers to transect kilometers; observed refers to # of whales observed; expected refers to # of whales expected if distribution were uniform throughout the study area; and χ^2 and p indicate results from permutation tests, which used individual whales as the sample unit. π_i represents the proportion of survey effort per depth zone, o_i is the proportion of whales observed in each depth zone, and $w_i = o_i/\pi_i$.

	Summer					Fall				
	Effort	Observed		Expected		Effort	Observed		Expected	
Depth zone (m)	(Tr km)	Bowhead	Beluga	Bowhead	Beluga	(Tr km)	Bowhead	Beluga	Bowhead	Beluga
Inner shelf-shallow (≤ 20 m)	8883	426	43	152	797	15 169	509	51	226	396
Inner shelf-deep (21–50 m)	19 431	360	227	332	1742	28 951	540	61	431	756
Outer shelf (51–200 m)	13 865	196	733	237	1243	21 021	242	668	313	549
Continental slope (201–2000 m)	14 050	77	4212	240	1260	17 587	31	1410	262	459
Basin (> 2000 m)	6073	6	372	104	545	6052	0	128	90	158
Total	62 304	1065	5587	1065	5587	88 782	1322	2318	1322	2318
				χ^2 = 400.47	9279.63				χ^2 = 575.64	2951.82
				p = 0.0064	0.4402				p = 0.0603	0.9682

		Bowhead whales		Beluga whales	
Depth zone (m)	π_i	o_i	w_i	o_i	w_i
Summer:					
Inner shelf-shallow (≤ 20 m)	0.143	0.400	2.797	0.008	0.056
Inner shelf-deep (21–50 m)	0.312	0.338	1.083	0.041	0.417
Outer shelf (51–200 m)	0.223	0.184	0.825	0.131	0.587
Continental slope (201–2000 m)	0.226	0.072	0.319	0.754	3.336
Basin (> 2000 m)	0.097	0.006	0.062	0.067	0.691
Total	1.000	1.000	5.086	1.000	5.087
Fall:					
Inner shelf-shallow (≤ 20 m)	0.171	0.385	2.251	0.022	0.129
Inner shelf-deep (21–50 m)	0.326	0.408	1.252	0.027	0.080
Outer shelf (51–200 m)	0.237	0.183	0.772	0.288	1.215
Continental slope (201–2000 m)	0.198	0.023	0.116	0.608	3.071
Basin (> 2000 m)	0.068	0.000	0.000	0.055	0.809
Total	1.000	1.000	4.391	1.000	5.303

Monthly Habitat Use, 2009–16

Results from the chi-squared permutation tests on depth distribution of individual bowhead whales were significant only for August and September, supporting the hypothesis of variable distribution with respect to depth; results for July and October suggested that the null hypothesis of uniform depth distribution could not be rejected (Table 3). Bowheads in July preferred outer shelf habitat (51–200 m; w_i = 2.070), with secondary preference for continental slope habitat (201–2000 m; w_i = 1.690; Table 3). In all remaining months, bowheads overwhelmingly preferred inner shelf-shallow habitat (≤ 20 m; August w_i = 3.162; September w_i = 2.313; October w_i = 2.168), with some preference for inner shelf-deep habitat in August and September.

For beluga whales, none of the monthly χ^2 permutation tests on depth distribution of number of individual belugas were significant (Table 4); however, all analogous tests conducted using sightings (groups) as the sample unit were significant in all months. Belugas preferred continental slope (201–2000 m depth) habitat in every month, with least preference for inner shelf in all months.

Comparison of monthly habitat selection ratios of bowhead and beluga whales indicated that the two species had almost no overlap in preferred habitat in any month. July was the only month during which some habitat preference overlapped, when bowheads used outer shelf and continental slope habitat (51–2000 m depth) and belugas used continental slope (201–2000 m depth).

Habitat Use Comparison, 1982–91 to 2009–16

Primary habitat preference results in the reanalyzed 1982–91 data remained similar in both seasons to those reported in Moore et al. (2000) for bowhead whales, but not for beluga whales (Table 5). The preferred depth habitat for belugas remained the same in fall, and preferred ice habitat in fall and depth habitat in summer varied only slightly, between the reanalyzed 1982–91 data and results reported in Moore et al. (2000). However, beluga ice habitat preference in summer differed considerably between Moore et al. (2000) and the reanalyzed 1982–91 dataset, with the former analysis indicating primary preference for open water/light ice (≤ 10%) cover and the reanalysis indicating a primary preference for moderately heavy ice (41%–70%) cover. The discrepancies noted are likely due to the use of whales instead of sightings as the sample unit in the reanalysis.

Permutation test results suggested that the depth distribution of bowhead whales was not uniform during September and fall in 1982–91 or during August, September, and summer in 2009–16. However, all of the

TABLE 3. Bowhead whales sighted on transect each month in the western Beaufort Sea, by depth zone, and depth selection ratios (w_i), for July–October, 2009–16. Details as in Table 2.

	July			August			September			October		
Depth zone (m)	(Tr km)	Observed Bowhead	Expected Bowhead	(Tr km)	Observed Bowhead	Expected Bowhead	(Tr km)	Observed Bowhead	Expected Bowhead	(tr km)	Observed Bowhead	Expected Bowhead
Inner shelf-shallow (≤ 20 m)	3150	7	19	5733	419	132	9285	322	139	5885	187	87
Inner shelf-deep (21–50 m)	6800	14	41	12 631	346	292	19 293	411	289	9658	129	142
Outer shelf (51–200 m)	4681	58	28	9184	138	212	13 381	117	201	7640	125	112
Continental slope (201–2000 m)	4941	50	30	9110	27	210	11 594	20	174	5993	11	88
Basin (> 2000 m)	2309	2	14	3764	4	87	4496	0	67	1557	0	23
Total	21 881	131	131	40 422	934	934	58 049	870	870	30 732	452	452
			$\chi^2 = 89.83$ $p = 0.4948$			$\chi^2 = 556.13$ $p = 0.0086$			$\chi^2 = 462.59$ $p = 0.0420$			$\chi^2 = 142.03$ $p = 0.2261$

	July			August			September			October		
Depth zone (m)	π_i	o_i	w_i	π_i	o_i	w_i	π_i	o_i	w_i	π_i	o_i	w_i
Inner shelf-shallow (≤ 20 m)	0.144	0.053	0.368	0.142	0.449	3.162	0.160	0.370	2.313	0.191	0.414	2.168
Inner shelf-deep (21–50 m)	0.311	0.107	0.344	0.312	0.370	1.186	0.332	0.472	1.422	0.314	0.285	0.908
Outer shelf (51–200 m)	0.214	0.443	2.070	0.227	0.148	0.652	0.231	0.134	0.580	0.249	0.277	1.112
Continental slope (201–2000 m)	0.226	0.382	1.690	0.225	0.029	0.129	0.200	0.023	0.115	0.195	0.024	0.123
Basin (> 2000 m)	0.106	0.015	0.142	0.093	0.004	0.043	0.077	0.000	0.000	0.051	0.000	0.000
Total	1.000	1.000	4.614	1.000	1.000	5.172	1.000	1.000	4.429	1.000	1.000	4.311

TABLE 4. Beluga whales sighted on transect each month in the western Beaufort Sea, by depth zone, and depth selection ratios (w_i) for July–October, 2009–16. Details as in Table 2.

	July			August			September			October		
Depth zone (m)	(Tr km)	Observed Beluga	Expected Beluga	(Tr km)	Observed Beluga	Expected Beluga	(Tr km)	Observed Beluga	Expected Beluga	(tr km)	Observed Beluga	Expected Beluga
Inner shelf-shallow (≤ 20 m)	3150	11	305	5733	32	492	9285	45	185	5885	6	222
Inner shelf-deep (21–50 m)	6800	86	658	12631	141	1085	19 293	30	385	9658	31	365
Outer shelf (51–200 m)	4681	353	453	9184	380	789	13 381	245	267	7640	423	289
Continental slope (201–2000 m)	4941	1464	478	9110	2748	782	11 594	714	231	5993	696	226
Basin (> 2000 m)	2309	202	223	3764	170	323	4496	123	90	1557	5	59
Total	21 881	2116	2116	40 422	3471	3471	58 049	1157	1157	30 732	1161	1161
			$\chi^2 = 2918.67$ $p = 0.8240$			$\chi^2 = 6456.51$ $p = 0.3050$			$\chi^2 = 1467.02$ $p = 0.9550$			$\chi^2 = 1601.38$ $p = 0.8860$

	July			August			September			October		
Depth zone (m)	π_i	o_i	w_i	π_i	o_i	w_i	π_i	o_i	w_i	π_i	o_i	w_i
Inner shelf-shallow (≤ 20 m)	0.144	0.005	0.035	0.142	0.009	0.063	0.160	0.039	0.244	0.191	0.005	0.026
Inner shelf-deep (21–50 m)	0.311	0.041	0.132	0.312	0.041	0.131	0.332	0.026	0.078	0.314	0.027	0.086
Outer shelf (51–200 m)	0.214	0.167	0.780	0.227	0.109	0.480	0.231	0.212	0.918	0.249	0.364	1.462
Continental slope (201–2000 m)	0.226	0.692	3.062	0.225	0.792	3.520	0.200	0.617	3.085	0.195	0.599	3.072
Basin (> 2000 m)	0.106	0.095	0.896	0.093	0.049	0.527	0.077	0.106	1.377	0.051	0.004	0.078
Total	1.000	1.000	4.905	1.000	1.000	4.722	1.000	1.000	5.701	1.000	1.000	4.724

TABLE 5. Summary of results for seasonal depth zone and sea ice cover habitat preferences of bowhead and beluga whales from Moore et al. (2000), the current reanalysis for 1982–91, and the current analysis for 2009–16.

Depth habitat:	1982–91[1]	1982–91 reanalysis[2] See Table 6	2009–16[2] See Table 6
Bowhead whales:			
Summer	Strongest association with continental slope and outer shelf habitats; least selection for inner shelf and basin habitats.	Very strong association with continental slope habitat; little selection of any other habitat.	Strongest association with inner shelf habitat; little selection for any other habitat.
Fall	Strongest association with inner shelf and outer shelf habitats; little selection for continental slope or basin.	Strongest association with inner shelf habitat, with some selection for outer shelf; little selection for continental slope or basin.	Strongest association with inner shelf habitat; little selection for any other habitat.
Beluga whales:			
Summer	Strongest association with continental slope and basin habitat; least selection for inner shelf.	Strongest association with basin and continental slope habitats; least selection for inner shelf.	Very strong association with continental slope; least selection for inner shelf.
Fall	Very strong association with continental slope habitat with some selection of basin and outer shelf; least selection for inner shelf.	Very strong association with continental slope habitat with some selection of outer shelf and basin; least selection for inner shelf.	Strongest association with continental slope habitat and outer shelf habitats; least selection for inner shelf.
Ice cover habitat:		See Table 7	See Table 7
Bowhead whales:			
Summer	Uniform distribution.	Strongest association with moderately light ice (11%–40%) habitat	Strongest association with open water/light ice (0%–10%); least selection for heavy ice (> 70%).
Fall	Strongest association with open water/light ice (0%–10%) habitat.	Strongest association with open water/light ice (0%–10%) habitat.	Strongest association with open water/light ice (0%–10%); least selection for moderately heavy ice (41%–70%), and no selection for heavy ice (> 70%).
Beluga whales:			
Summer	Strongest association with open water/light ice (0%–10%), heavy ice (> 70%), and moderately heavy ice (41%–70%) habitat; least selection for moderately light ice (11%–40%).	Strongest association with moderately heavy ice (41%–70%) and heavy ice (> 70%) habitat; least selection for moderately light ice (11%–40%).	Strongly associated with moderately light ice (11%–40%); least selection for heavy ice (> 70%).
Fall	Strongest association with moderately heavy ice (41%–70%) and heavy ice (>70%); least selection for open water/light ice (%–10%).	Strongest association with heavy ice (> 70%) and moderately heavy ice (41%–70%); least selection for open water/light ice (0%–10%).	Strongest association with open water/light ice (0%–10%); least association with moderately light ice (11%–40%).

[1] Data summarized from Moore et al. (2000).
[2] Data summarized in this study.

standard chi-squared tests on bowhead whale sightings suggested that distribution by depth was not uniform in any month or season of either period. In summer 1982–91, primary bowhead depth preference was for continental slope habitat (201–2000 m; $w_i = 2.678$), while in summer 2009–16, bowheads preferred inner shelf habitat ($w_i = 1.658$; Table 6**)**. In fall, bowheads used similar habitat during both periods: inner shelf habitat (≤ 50 m) was used most often (1982–91, $w_i = 1.474$; 2009–16, $w_i = 1.661$) and basin habitat was used the least (1982–91, $w_i = 0.104$; 2009–16, no use of basin) (Table 6).

For beluga whales, monthly and seasonal permutation test results of depth distribution were not significant in either period; however, all of the standard chi-squared tests using sightings as the sample unit were significant. In summer, beluga habitat preference was for basin (> 2000 m depth; $w_i = 1.660$) in the reanalyzed 1982–91 dataset and for continental slope (201–2000 m; $w_i = 3.300$) in 2009–16 (Table 6). In fall, belugas preferred continental slope habitat (201–2000 m) during both periods (1982–91, $w_i = 2.942$; 2009–16, $w_i = 3.091$) (Table 6). Belugas were least likely to use inner shelf habitat in both summer and fall.

TABLE 6. Comparison of seasonal depth zone selection ratios (w_i) for bowhead and beluga whales in 1982–91 and 2009–16. π_i represents the proportion of survey effort per depth zone, o_i is the proportion of whales observed in each depth zone, and $w_i = o_i/\pi_i$. Tr km refers to transect kilometers; # observed refers to number of whales observed. Note that total Tr km in Tables 6 and 7 differ because different methods were used to summarize effort.

1982–91: **Summer**	Effort (Tr km)	π_i	Bowhead whales # observed	Bowhead whales o_i	Bowhead whales w_i	Belugas # observed	Belugas o_i	Belugas w_i
Depth zone								
Inner shelf (≤ 50 m)	15 393	0.306	10	0.081	0.264	33	0.078	0.256
Outer shelf (51–200 m)	9668	0.192	19	0.153	0.798	54	0.128	0.667
Continental slope (201–2000 m)	12 283	0.244	81	0.653	2.678	154	0.365	1.496
Basin (> 2000 m)	13 014	0.258	14	0.113	0.437	181	0.429	1.660
Total	50 360	1.000	124	1.000	4.177	422	1.000	4.078
Fall	Effort (Tr km)	π_i	# observed	o_i	w_i	# observed	o_i	w_i
Depth zone								
Inner shelf (≤ 50 m)	75 713	0.487	498	0.719	1.474	63	0.020	0.041
Outer shelf (51–200 m)	35 139	0.226	153	0.221	0.976	1004	0.322	1.421
Continental Slope (201–2000 m)	27 170	0.175	34	0.049	0.280	1607	0.515	2.942
Basin (> 2000 m)	17 297	0.111	8	0.012	0.104	448	0.143	1.289
Total	155 320	1.000	693	1.000	2.834	3122	1.000	5.694
2009–16: **Summer**	Effort (Tr km)	π_i	# observed	o_i	w_i	# observed	o_i	w_i
Depth zone								
Inner shelf (≤ 50 m)	28 314	0.454	829	0.754	1.658	282	0.050	0.110
Outer shelf (51–200 m)	13 865	0.223	180	0.164	0.735	759	0.134	0.603
Continental slope (201–2000 m)	14 050	0.226	86	0.078	0.347	4211	0.744	3.300
Basin (> 2000 m)	6073	0.097	5	0.005	0.047	407	0.072	0.738
Total	62 304	1.000	1100	1.000	2.740	5659	1.000	4.750
Fall	Effort (Tr km)	π_i	# observed	o_i	w_i	# observed	o_i	w_i
Depth zone								
Inner shelf (≤ 50 m)	44 121	0.497	1143	0.825	1.661	112	0.048	0.097
Outer shelf (51–200 m)	21 021	0.237	209	0.151	0.637	663	0.285	1.205
Continental slope (201–2000 m)	17 587	0.198	33	0.024	0.120	1423	0.612	3.091
Basin (> 2000 m)	6052	0.068	0	0.000	0.000	126	0.054	0.795
Total	88 782	1.000	1385	1.000	2.418	2324	1.000	5.188

As for distribution with respect to sea ice concentration, permutation test results suggested that for both species, these distributions were not uniform during any season in either period. Standard chi-squared test results on the number of sightings in each sea ice concentration also indicated non-uniform seasonal distributions for both species and periods, except for bowhead whales during summer 1982–91 ($p = 0.17$). In fall 1982–91, bowheads were primarily associated with open water/light ice (≤ 10%; $w_i = 1.724$) (Table 7). In 2009–16, bowhead whales were also primarily associated with open water/light ice (≤ 10%) habitat in both summer ($w_i = 1.462$) and fall ($w_i = 1.080$) (Table 7). For beluga whales, ice cover association differed between periods in both summer and fall. In summer, belugas were primarily associated with moderately heavy ice (41%–70%; $w_i = 1.243$) in 1982–91, compared to moderately light ice (11%–40%; $w_i = 1.644$) in 2009–16 (Table 7). In fall, the difference between 1982–91 and 2009–16 was more dramatic: belugas were associated with heavy ice (> 70%) in fall 1982–91 ($w_i = 1.748$), but with open water/light ice (≤ 10%) in 2009–16 ($w_i = 1.079$). The relationship with sea ice is likely an association only and not active selection by belugas. Belugas were found along the continental slope during both time periods, and the slope was characterized by heavier ice in 1982–91 and by open water/light ice in 2009–16.

DISCUSSION

Data collected on whales and other marine mammals in the western Beaufort Sea as part of the ASAMM project and its precursors span more than 30 years. Changes to the Arctic climate over the past several decades, including the loss of seasonal sea ice, increased ocean and air temperatures, and greater oceanic freshwater content, are well documented (e.g., Johannessen and Miles, 2011; Woodgate et al., 2012; Cohen et al., 2014; Wood et al., 2015). In this paper we analyzed bowhead and beluga whale sighting data obtained during aerial surveys conducted

TABLE 7. Comparison of seasonal sea ice cover selection ratios (w_i) for bowhead and beluga whales in 1982–91 and 2009–16. Details as in Table 6.

	Effort		Bowhead whales			Beluga whales		
	(Tr km)	π_i	# observed	o_i	w_i	# observed	o_i	w_i
1982–91:								
Summer								
Ice cover category (%)								
≤ 10%	11 751	0.235	30	0.242	1.030	83	0.197	0.837
11%–40%	5922	0.118	20	0.161	1.362	28	0.066	0.560
41%–70%	7057	0.141	17	0.137	0.972	74	0.175	1.243
71%–100%	25 290	0.506	57	0.460	0.909	237	0.562	1.111
Total	50 020	1.000	124	1.000	4.273	422	1.000	3.751
Fall								
Ice cover category (%)								
≤ 10%	73 046	0.474	566	0.817	1.724	599	0.192	0.405
11%–40%	14 493	0.094	18	0.026	0.276	226	0.072	0.770
41%–70%	19 606	0.127	36	0.052	0.409	631	0.202	1.590
71%–100%	47 082	0.305	73	0.105	0.345	1666	0.534	1.748
Total	154 227	1.000	693	1.000	2.755	3122	1.000	4.513
2009–16:								
Summer								
Ice cover category (%)								
≤ 10%	41 841	0.646	1038	0.944	1.462	3214	0.568	0.880
11%–40%	14 466	0.223	36	0.033	0.147	2077	0.367	1.644
41%–70%	5180	0.080	23	0.021	0.262	236	0.042	0.522
71%–100%	3323	0.051	3	0.003	0.053	132	0.023	0.455
Total	64 810	1.000	1100	1.000	1.923	5659	1.000	3.501
Fall								
Ice cover category (%)								
≤ 10%	81 843	0.912	1364	0.985	1.080	2286	0.984	1.079
11%–40%	4078	0.045	20	0.014	0.318	9	0.004	0.085
41%–70%	1304	0.015	1	0.001	0.050	15	0.006	0.444
71%–100%	2515	0.028	0	0.000	0.000	14	0.006	0.215
Total	89 740	1.000	1385	1.000	1.447	2324	1.000	1.823

in the western Beaufort Sea in 2009–16 and replicated the analyses of habitat preference in 1982–91 originally conducted by Moore et al. (2000) to compare habitat preference during this period of great change in the Arctic environment (Jeffries et al., 2013). These results also provide complementary analyses to those for bowhead and gray whales in the eastern Chukchi Sea (Clarke et al., 2016).

Aerial survey protocols used in 2009–16 replicated those used during 1982–91 as closely as possible, and consistent methods were used in the habitat use analyses conducted for both periods. However, as noted in Clarke et al. (2016), several caveats pertaining to ASAMM data collection in 1982–91 and 2009–16 have the potential to affect interpretation of results. These caveats, in brief, include improved accuracy and precision of field data, more precise and accurate delineation of depth zones in 2009–16, and differences in the temporal and spatial extent of data analyzed, the amount of sea ice cover, and the aerial platforms used in 1982–91 and in 2009–16. Collectively, the differences in data and sampling protocols and platforms between 1982–91 and 2009–16 compromise direct comparison of sighting rates and underscore the importance of using habitat selection ratios from within each survey period to provide comparisons across time.

Shifting Phenology of Bowhead Whales

Changes in distribution, relative abundance, and habitat preference suggest that bowhead whales now occur earlier and in greater numbers in the western Beaufort Sea than they did in the 1980s. More bowheads were seen in summer and fall 2009–16 (1100 and 1385, respectively) than in summer and fall 1982–91 (124 and 693, respectively); the higher totals in fall 2009–16 occurred despite 58% less survey effort in those years (Tables 6 and 7). The proliferation of bowhead whales observed in 2009–16 may be due to several factors, including better detection probabilities from a survey aircraft traveling at a slower speed and outfitted with bubble windows; a much larger Bering-Chukchi-Beaufort bowhead population: 16 892 (CV = 0.244; Givens et al., 2013) in 2011 compared to 6928 (CV = 0.120; Zeh and Punt, 2005) in 1988; changes in behavior which may have affected detection rate; or a combination of these and other factors.

TABLE 8. Comparison of monthly depth zone selection ratios (w_i) for bowhead whales in 1982–91 and 2009–16. Details as in Table 6.

July	1982–91 Effort (Tr km)	π_i	Bowhead whales # observed	o_i	w_i	2009–16 Effort (Tr km)	π_i	Bowhead whales # observed	o_i	w_i
Depth zone										
Inner shelf (≤ 50 m)	505	0.155	0	NA	NA	9950	0.455	22	0.157	0.346
Outer shelf (51–200 m)	847	0.259	0	NA	NA	4681	0.214	56	0.400	1.870
Continental slope (201–2000 m)	913	0.279	0	NA	NA	4941	0.226	60	0.429	1.898
Basin (> 2000 m)	1004	0.307	0	NA	NA	2309	0.106	2	0.014	0.135
Total	3269	1.000	0	NA	NA	21 881	1.000	140	1.000	4.249
August	Effort (Tr km)	π_i	Bowhead whales # observed	o_i	w_i	Effort (Tr km)	π_i	Bowhead Whales # observed	o_i	w_i
Depth zone										
Inner shelf (≤ 50 m)	14 888	0.316	10	0.081	0.255	18 364	0.454	807	0.841	1.850
Outer shelf (51–200 m)	8822	0.187	19	0.153	0.818	9184	0.227	124	0.129	0.569
Continental slope (201–2000 m)	11 370	0.241	81	0.653	2.705	9110	0.225	26	0.027	0.120
Basin (> 2000 m)	12 011	0.255	14	0.113	0.443	3764	0.093	3	0.003	0.034
Total	47 091	1.000	124	1.000	4.221	40 422	1.000	960	1.000	2.573
September	Effort (Tr km)	π_i	Bowhead whales # observed	o_i	w_i	Effort (Tr km)	π_i	Bowhead whales # observed	o_i	w_i
Depth zone										
Inner shelf (≤ 50 m)	40 521	0.447	342	0.758	1.696	28 578	0.492	775	0.863	1.753
Outer shelf (51–200 m)	19 142	0.211	78	0.173	0.819	13 381	0.231	100	0.111	0.483
Continental slope (201–2000 m)	17 139	0.189	23	0.051	0.270	11 594	0.200	23	0.026	0.128
Basin (> 2000 m)	13 833	0.153	8	0.018	0.116	4496	0.077	0	0.000	0.000
Total	90 636	1.000	451	1.000	2.901	58 049	1.000	898	1.000	2.364
October	Effort (Tr km)	π_i	Bowhead whales # observed	o_i	w_i	Effort (Tr km)	π_i	Bowhead whales # observed	o_i	w_i
Depth zone										
Inner shelf (≤ 50 m)	35 192	0.544	156	0.645	1.185	15 542	0.506	368	0.756	1.494
Outer shelf (51–200 m)	15 996	0.247	75	0.310	1.253	7640	0.249	109	0.224	0.900
Continental slope (201–2000 m)	10 031	0.155	11	0.045	0.293	5993	0.195	10	0.021	0.105
Basin (> 2000 m)	3464	0.054	0	0.000	0.000	1557	0.051	0	0.000	0.000
Total	64 684	1.000	242	1.000	2.731	30 732	1.000	487	1.000	2.500

Bowhead whales occurred earlier in the western Beaufort Sea in the recent surveys than they did 30 years ago. Bowhead distribution in summer 2009–16 was also much broader than that observed in 1982–91, particularly when assessed by month instead of by season. Bowheads were not seen in the western Beaufort in July 1982–91 (although this may reflect limited survey effort), while bowhead distribution in July 2009–16 closely resembled the distribution in August 1982–91 (Fig. 3A; Moore et al., 2000: Fig. 5): bowheads were seen farther from shore and primarily in the eastern Alaskan Beaufort Sea (140˚ W to 148˚ W). Bowhead whale distribution in August 2009–16 (Fig. 3A) was similar to the distribution in fall 1982–91 (Moore et al., 2000: Fig. 5) and fall 2009–16 (Fig. 3B), when bowheads were observed across the entire western Beaufort Sea on the inner shelf.

Finally, depth zone habitat preference per month in 2009–16 indicated a preference for deeper water (outer shelf and continental slope) in July and shallower water (inner shelf) from August through October (Table 8). This shift in depth preference occurred later in 1982–91, from deeper habitat in August to shallower habitat in September-October (Moore et al., 2000).

These results suggest that, in most years, some bowheads may now travel to or remain in the western Beaufort Sea inner shelf earlier in summer than in the 1980s. Bowhead occurrence on the inner shelf of the western Beaufort Sea in August (in addition to September and October) may be related to increased opportunities for feeding that were not present 30 years ago because there were significantly fewer open water days, or it may reflect the expansion of a larger population to previously marginal areas. Moore and Stabeno (2015) suggested that bowheads may benefit from biophysical changes that have occurred in the Pacific Arctic, including ice-free summers, warmer currents, and increased upwelling and primary production. The most dramatic reduction in sea ice cover in the Western Arctic during the open water season occurred in the western Beaufort Sea: the number of open water days has been increasing by 20 days per decade since 1979 (Druckenmiller et al., 2017). Bowhead whales may also be moving into the inner shelf of the western Beaufort Sea earlier than they were 30 years ago to avoid increased prey competition elsewhere on their summer feeding grounds. The stock is currently estimated to be at least 2.5 times as large as it was in the late 1980s (Givens et al., 2013), and in some years the eastern Beaufort Sea ecosystem may not produce enough prey for this larger bowhead population. Harwood et al. (2010), on the basis of aerial surveys conducted in the eastern Beaufort Sea in late August 2007 – 09, indicated that bowheads may be aggregating there earlier than they were in the 1980s, perhaps by two weeks. While bowheads in general may not use the same eastern Beaufort Sea aggregation areas each year (Harwood et al., 2010), perhaps because of interannual differences in oceanographic conditions that concentrate bowhead whale prey (Walkusz et al., 2010, 2012), some individuals do exhibit site fidelity in successive years (Harwood et al., 2017). Unpredictable or sub-optimal prey sources in both nearshore and offshore areas of the eastern Beaufort Sea and Amundsen Gulf in some years could compel a larger bowhead population to look elsewhere (e.g., the western Beaufort Sea) for denser prey aggregations.

Availability of prey may also affect the distribution by age class of bowhead whales in the eastern Beaufort Sea. Satellite telemetry results specific to the eastern Beaufort Sea suggest that immature bowheads are more likely than mature whales to use the aggregation areas on the eastern Beaufort Sea shelf (Harwood et al., 2017). Larger, older bowheads are more likely to be found farther east in Amundsen Gulf and in deeper water areas farther offshore in the eastern (Koski et al., 1988) and central Beaufort Sea (Koski and Miller, 2009), perhaps because they are physiologically better adapted to feeding in deeper waters (Koski and Miller, 2002). It is also possible that larger bowheads, because of the combination of energy stores in the lipids of their thick blubber and low metabolic rates (George, 2009), do not need to feed every year and can remain in less productive areas. Data analyzed in this paper do not incorporate the influence of bowhead whale size and age on distribution or habitat preference. With few exceptions (e.g., a calf closely associated with a larger whale assumed to be its mother, or whales with completely white flukes that are likely very mature adults), bowhead whales are generally not specifically identified to size or age in the ASAMM database. Determining size and age without photogrammetry is subjective. Photogrammetry has never been an objective of ASAMM surveys and therefore was never integrated into survey protocols. Variable seasonal use of the western Beaufort Sea by different age and size classes of bowhead whales has been well documented (Koski and Miller, 2009). It is possible that some of the changes documented over 35 years during this study were related to changes in how various age and sex classes use the western Beaufort Sea within and between years. Investigating this idea further would require dedicated photogrammetric aerial surveys that use calibrated photographic techniques similar to the surveys conducted on bowhead whales in the 1980s and 1990s (Koski and Miller, 2009) or the use of unmanned aircraft systems similar to those used on killer whales near Vancouver Island, British Columbia (Durban et al., 2015).

Feeding was noted nearly every year ASAMM surveys were conducted, but with considerable interannual variability. Two of the years with high summer sighting rates (2014 and 2016; Fig. 4A) were years in which large groups of bowhead whales were feeding in the western Beaufort Sea in August. Results from ASAMM and satellite telemetry studies have shown that bowhead whale feeding opportunities in the western Beaufort Sea in summer and fall are ephemeral (Citta et al., 2015; Clarke et al., 2015). Results from telemetry studies (2006 – 12) denoted no core-use areas between the Tuktoyaktuk Shelf in the Canadian Beaufort Sea and the Point Barrow area in the western Alaskan Beaufort Sea (Citta et al., 2015), although aerial survey data from 2007 – 12 identified bowhead whale hotspots that may be related to feeding aggregations (Kuletz et al., 2015). Their energetic requirements dictate that bowheads forage in areas of densely aggregated zooplankton, including copepods, euphausiids, mysids, and amphipods (Lowry, 1993; Lowry et al., 2004). Environmental factors such as earlier sea ice retreat and warmer sea temperatures (Frey et al., 2015) can result in increased primary and secondary productivity (Moore and Laidre, 2006; Arrigo et al., 2008; Arrigo and van Dijken, 2015; Grebmeier et al., 2015), which improve the potential for feeding hotspots. Increased advection (Pickart, 2004) and increased freshwater river drainage and upwelling-favorable winds can create fronts that aggregate bowhead whale prey (Ashjian et al., 2010; Moore et al., 2010; Okkonen et al., 2011, 2017; Carmack et al., 2016). The extent and frequency with which these factors occur in the eastern and western Beaufort Sea during any given open water season differ annually. If the oceanographic mechanisms needed for bowhead prey aggregation do not occur, feeding opportunities may not transpire or may be so limited as to go undetected during aerial surveys. Interannual variability of feeding opportunities may also lead to less predictability in bowhead summer and fall movements because of the fluctuating quality and quantity of feeding areas throughout the Beaufort Sea (Druckenmiller et al., 2017).

The co-occurrence of several foraging-positive environmental factors likely led to the relatively high numbers of bowhead whales seen feeding from Camden Bay to Point Barrow in August 2016. National Center for Environmental Protection Reanalysis wind data indicated a lack of upwelling winds near Cape Bathurst, Canada, from mid-July through early August (NOAA Earth Science Research Laboratory, 2016), which may have dampened bowhead prey production there and triggered an earlier-than-usual exodus of bowheads from the eastern Beaufort Sea. A similar lack of upwelling near Cape Bathurst that occurred in late July and most of August 2013 coincided with higher-than-normal bowhead sighting rates in the western Beaufort Sea (Clarke et al., 2017). The largest aggregation of bowheads ever observed during a single ASAMM survey was composed of 498 whales seen on the inner shelf of Harrison Bay on 26 August 2016. Although that bay had not previously been identified as a bowhead feeding area (ASAMM data; Citta et al., 2015; Kuletz et al., 2015), 87% of the bowheads observed on 26 August were feeding. A frontal system that formed in Harrison Bay in late August 2016, likely as a result of record high freshwater discharge from the Colville River (USGS National Water Information System, 2016), in combination with upwelling-favorable winds (NOAA National Data Buoy Center, 2016; Weather Underground, 2016), probably aggregated bowhead prey. Similar conditions were documented in the central Alaskan Beaufort Sea in September 2014 (Okkonen et al., 2017), when large groups of feeding bowhead whales were observed near shore between 144˚ W and 150˚ W.

Beluga Whales – Predictable Occurrence

Beluga whale distribution and relative density illustrated the importance of continental slope habitat in the western Beaufort Sea, particularly in summer. In 2009 – 16, sighting rates for all years pooled together were more than three times as high in summer as in fall (Table 1). Sighting rates were lower and distribution sparse in fall 2009 – 16 except in the area near Barrow Canyon. The importance of Barrow Canyon habitat for belugas is well documented via data from passive acoustic monitoring, satellite telemetry, and aerial surveys (Richard et al., 2001; Suydam et al., 2001; Suydam, 2009; Stafford et al., 2013, 2017; Hauser et al., 2015, 2016; Kuletz et al., 2015).

ASAMM surveys do not completely encompass areas that have been identified as core concentration areas in the western Beaufort Sea for both the EBS and ECS beluga stocks (Hauser et al., 2014, 2016). Lowry et al. (2017) estimated that the average proportion of days that tagged ECS belugas spent in the western Beaufort study area in summer (19 July to 20 August) was 0.35 (CV = 0.83) for males and 0.64 (CV = 0.49) for females. In fall, locations of tagged belugas from both stocks within the ASAMM western Beaufort study area were between 0% and approximately 25% (D. Hauser, pers. comm. 2017). This pattern would indicate that the majority of belugas from both stocks are not present in the ASAMM study area in either summer or fall. Conducting aerial surveys throughout all core areas is not logistically or economically feasible. Results from satellite telemetry (Richard et al., 2001; Suydam et al., 2001) and passive acoustic monitoring (Garland et al., 2015; Stafford et al., 2016) provide insights into beluga occurrence and migration timing in areas beyond the ASAMM study area. Collaborative syntheses using data from several complementary sources (e.g., Stafford et al., 2013, 2017; Hauser et al., 2016) continue to be essential to improving our understanding of Pacific Arctic belugas.

The proportion of beluga whales in the western Beaufort Sea study area in any given year is unknown. Annual beluga sighting rates varied from a low of 0.0055 whales/km in 2010 to a high of 0.0652 whales/km in 2014, a more than tenfold difference. Annual variability in beluga relative density in the western Beaufort Sea is likely related to several factors that are largely unknown in any given year. These factors may include the proportion of the ECS beluga stock that migrates into the eastern Beaufort Sea in spring and early summer, the proportions of EBS and ECS stocks that use the western Beaufort study area, the timing of the onset of the westbound migration, foraging opportunities, presence of potential predators, and overall population sizes. Differentiating between beluga stocks is not possible during aerial surveys, but analysis of satellite telemetry data suggest that belugas observed in the western Beaufort Sea in July and August are likely from the ECS stock (Hauser et al., 2014). The easterly swim direction of belugas observed by ASAMM in the Barrow Canyon area in summer suggests that they are likely ECS belugas migrating into the western Beaufort Sea. The EBS stock remains in the eastern Beaufort Sea through August, migrates across the western Beaufort Sea in September and into the Chukchi Sea in October. Hauser et al. (2016) analyzed beluga satellite telemetry data divided into an early period (1993 – 2002) and a late period (2004 – 12) for both the ECS and EBS stocks, and found that the two stocks responded differently to changes in the ecosystem (i.e., sea ice loss in the late period). The ECS stock remained in the Pacific Arctic region later in fall during the late period compared to belugas tagged during the early period, and migration out of the western Beaufort Sea was positively correlated with sea ice freeze-up in fall. Conversely, there was no significant change to migration timing and no correlation with ice freeze-up for EBS belugas in the Beaufort Sea region. From the most recent population estimates for the two stocks (2012 ECS estimate of 20 752 belugas, Lowry et al., 2017; 1999 EBS estimate of 39 258 belugas, Hill and DeMaster, 1999), we might expect sighting rates to be highest in September in the western Beaufort Sea because the EBS stock is larger, but we found the opposite: September had the lowest sighting rate of all months. Size-at-age and blubber thickness in the EBS stock each showed slight decreases through 2008 (Harwood et al., 2014), and it is possible that the EBS population is no longer as large as the 1999 estimate indicated.

Habitat Partitioning and Preference

Habitat partitioning by depth between bowhead and beluga whales was documented in Moore et al. (2000) for data collected in 1982 – 91 and remained evident in 2009 – 16. While some overlap occurred in sighting distribution, habitat selection ratios indicated that species co-occurrence was minimal in all months except July, when both species showed preference for deeper waters (51 – 2000 m for bowheads, 201 – 2000 m for belugas). Data collected via satellite-tagged whales identified six core-use areas for bowheads (Citta et al., 2015) and numerous core areas for ECS and EBS belugas (Hauser et al., 2014), but the only temporal and geographic overlap between the two species occurred in the Barrow Canyon area.

Change in bowhead habitat preference from 1982–91 to 2009–16 was limited to depth preference in summer (discussed above), while change in beluga habitat preference was limited to sea ice cover in fall. Sea ice cover preference changed from heavy ice cover in 1982–91 to open water/light ice cover in 2009–16, which was not surprising in view of the relative lack of sea ice cover during 2009–16 (Table 7). Beluga depth preference was consistently for continental slope or basin zones during both time periods, indicating that the static habitat (depth) was more persistent than the variable habitat (ice). Put another way, the relationship of belugas to sea ice cover in the western Beaufort Sea was likely altered because sea ice cover changed, not because beluga distribution changed. Similarly, Hauser et al. (2017) found that satellite-tagged belugas from 1993 to 2012 selected seasonal habitat based on depth, slope, and proximity to bathymetric features like Barrow Canyon more than on sea ice variables, which rarely acted as the primary drivers of habitat use in summer or fall.

Chi-squared permutation tests could not reject the hypothesis of uniform density of whales with respect to depth for many of the bowhead analyses or for any of the beluga analyses. In contrast, all of the standard chi-squared tests on bowhead and beluga whale sightings suggested that these species' monthly and seasonal distributions were not uniform with respect to depth in either period. The apparent contradictory conclusions from the analyses based on number of whales vs. number of sightings imply that there is variability in clustering (group size) across the depth zones during both periods. For example, there were relatively large groups of belugas in the outer shelf (particularly near Barrow Canyon) during 2009–16 that likely minimized the difference between the observed and expected number of whales (under the assumption of uniform density) in this stratum, which had a relatively low number of sightings.

Limitations of the Dataset

The ASAMM line-transect aerial surveys were designed to cover a broad geographic area while monitoring the bowhead whale migration in the western Beaufort Sea in areas of interest to the petroleum industry. By necessity, survey effort was limited both to areas of acceptable survey conditions and by aircraft fuel reserves, and these surveys have never incorporated focal animal-following protocols during which extensive behavioral observation sessions are conducted to record behaviors of multiple animals (Richardson et al., 1985; Würsig et al., 1985; Robertson et al., 2013). ASAMM observers are afforded only a brief time (approximately 30–45 seconds) to determine the behavior of each animal or group of animals. Whale behavior can be ambiguous, and establishing whale "activity" is difficult. For example, whales that are milling at the surface may be socially interacting with other whales, or staying at the surface between feeding dives, or both. Some behaviors, including water-column or near-bottom feeding, are nearly impossible to detect during aerial surveys. Unless an observer can definitively determine that a whale or group of whales is engaged in a specific activity (e.g., resting, feeding, breaching), the behavior is generally recorded as "swim," although it is quite possible that that whale was engaged in other behaviors that were not obvious during a brief overflight. Seasonality has occasionally been used to assist with defining bowhead whale activity (summer = feeding; fall = migrating), but data collected during aerial surveys (this study and others) and from satellite-telemetered whales (Citta et al., 2015) have shown that behavior cannot be assumed on the basis of season.

The degree to which anthropogenic activity affected whale behavior in the western Beaufort Sea cannot be quantified from ASAMM survey data. Anthropogenic activities, which may include seismic operations, offshore drilling, and vessel traffic varying in size from small boats to icebreakers and cruise ships, have been shown to affect bowhead and beluga whale behavior in other studies (Richardson et al., 1985, 1986, 1990; Lesage et al., 1999; Blackwell et al., 2013, 2015). In some years anthropogenic activity appeared more extensive (e.g., in 2012, when offshore drilling occurred in the central Alaskan Beaufort Sea; Bisson et al., 2013), but reliable assessments of when and where commercial, seismic, and recreational activity occurred in the Beaufort Sea in most years are not available. Reeves et al. (2014), for example, included a summary figure of shipping in the Arctic in 2012 based on the activity of all vessels outfitted with Automatic Identification System (AIS) transponders. The figure shows almost no activity in the western Beaufort Sea when, in fact, 11 vessels traveled more than 38 000 km from mid-August through late October as part of the Shell drilling operation (Patterson et al., 2013). Those activities were likely not included in the Reeves et al. (2014) figure, either because the Shell vessels did not have AIS transponders or because information from the transponders was not available.

Sighting rates derived from ASAMM data represent relative density, and at present, they cannot be corrected to provide absolute density for lack of correction factors related to availability bias specific to the Turbo Commander, the aircraft type used for most of the 2009–16 surveys. Starting in 2018, ASAMM survey protocols will be enhanced to collect the data necessary to calculate availability bias. In addition, dive data from satellite-telemetered bowhead whales in 2007–12 are being analyzed for surface and dive time intervals (J. Citta, pers. comm. 2017). Furthermore, analyses to determine perception bias are currently underway.

SUMMARY AND CONCLUSIONS

In 2009–16, bowhead whales in the western Beaufort Sea were found on the continental slope in mid-July, moved into nearshore inner shelf waters by August, and remained on the inner shelf through September and October. Use of the western Beaufort Sea by bowheads has therefore shifted to approximately one month earlier compared to 30 years ago. Bowheads use the western Beaufort Sea inner shelf for migrating between the eastern Beaufort Sea and the northwestern Chukchi Sea, but when environmental conditions aggregate prey, bowheads take advantage of those conditions to feed and may be found in very large groups in some years. Bowhead feeding in the western Beaufort Sea is nonexistent in some years and a dominant behavior in other years, and the presence of large feeding groups has a strong effect on relative density. Diminished sea ice cover has likely indirectly affected bowhead whale distribution, migratory timing, and habitat preference by decreasing foraging opportunities in the eastern Beaufort Sea and possibly increasing productivity in the western Beaufort Sea in some years.

Beluga whales in 2009–16 remained offshore in continental slope habitat in summer and fall, as had been observed in 1982–91. The sighting rate in summer 2009–16 was three times as great as in fall 2009–16. ECS and EBS belugas both would be expected to occur west of 140˚ W, but it is likely that the majority of belugas from both stocks spend greater proportions of time in basin waters, beyond the extent of the ASAMM study area. Beluga depth preference remained identical over a span of more than 30 years. Sea ice cover does not appear to have had a strong effect on beluga distribution and migratory timing in the western Beaufort Sea.

Multiyear monthly and seasonal analyses of aerial survey data are necessary to detect trends and track changes that are occurring in the western Beaufort Sea ecosystem. The shift to earlier occurrence of bowhead whales (from August to July) and the continued use of the continental slope by beluga whales in summer are two phenomena recorded in the western Beaufort Sea over a 30-year time span. Aerial surveys conducted in the western Beaufort Sea in summer and fall 2009–16 also documented considerable interannual variability in distributions, sighting rates, and behaviors of bowhead and beluga whales, emphasizing the continued importance of annual sampling. The eastern boundary of the study area (140˚ W) is arbitrary with regard to whales and ecosystems; broadening survey coverage to simultaneously cover the western and eastern parts of the Beaufort Sea would be beneficial in documenting the effects of ecosystem changes on bowhead and beluga whales throughout the Beaufort Sea environment.

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