ARCTIC
VOL. 62, NO. 2 (JUNE 2009) P. 137–150

Habitat Use by Different Size Classes of Bowhead Whales in the Central Beaufort Sea during Late Summer and Autumn

WILLIAM R. KOSKI[1] and GARY W. MILLER[2]

(*Received 2 January 2008; accepted in revised form 11 September 2008*)

ABSTRACT. The frequency distributions of bowhead whale (*Balaena mysticetus*) size classes were studied as functions of year, location, water depth, and date. Whales were classified by size and status as calves, small subadults (non-calves < 10 m); large subadults (10–13 m); and adults (> 13 m). Adults include mothers with calves, which were also counted separately. During mid-August to early October of 1982, 1984–86, and 1998–2000, calibrated vertical photography was used to obtain known-scale images of 901 different whales in waters up to 200 m deep between Flaxman and Herschel islands (146˚ to 139˚ W) in the central Beaufort Sea. Age composition of the whales photographed over all years of our study was calves 6.2%, small subadults 31.4%, large subadults 33.3%, and adults 29.1%. We found proportionally more subadults and fewer adults than are estimated to be in the overall population, and this result was found both before and after making allowance for reduced effort to obtain photographs early and late in the migration period. Thus parts of the central Beaufort Sea up to 200 m deep appear to be more heavily used by subadult bowheads than by adults in most years. Significant interannual variation existed in length-frequency distributions of whales among years, geographic subdivisions of the study area, water depth categories, and time periods. This variation was due to variable use of the study area by each size class in different years, differences in the water depths used by different size classes, and different migration timing by each size class. In all years, small subadult whales were the dominant group in shallow (< 20 m) nearshore habitats, and the size of the whales increased with increasing water depth. Timing of movements into and through the study area were also related to size class: small subadults arrived first in late August and departed in late September, and adults arrived last in late September. Mothers and calves arrived in early September and were common until at least early October.

Key words: bowhead whale, *Balaena mysticetus*, habitat use, photogrammetry, lengths, feeding, autumn migration, water depth, date, annual variation, productivity

RÉSUMÉ. La répartition des fréquences de la baleine boréale (*Balaena mysticetus*) en fonction des classes de dimensions a été étudiée à la lumière de critères tels que l'année, l'emplacement, la profondeur de l'eau et la date. Les baleines étaient classées d'après leurs dimensions et leur état, comme suit : baleineaux, petites baleines immatures (non-baleineaux < 10 m); grosses baleines immatures (10–13 m); et baleines adultes (> 13 m). Les adultes comprenaient les mères avec leurs baleineaux, qui étaient aussi comptés séparément. De la mi-août au début octobre 1982, 1984 à 1986 et 1998 à 2000, nous nous sommes servi de photographies verticales calibrées pour obtenir des images d'échelle connue de 901 baleines différentes dans des eaux pouvant atteindre une profondeur de 200 m entre les îles Flaxman et Herschel (146˚ à 139˚O), dans le centre de la mer de Beaufort. La composition par âge des baleines photographiées au cours de toutes les années visées par l'étude s'établissait comme suit : 6,2 % de baleineaux, 31,4 % de petites baleines immatures, 33,3 % de grosses baleines immatures et 29,1 % de baleines adultes. De manière proportionnelle, nous avons repéré plus de baleines immatures et moins de baleines adultes comparativement aux estimations de telles baleines au sein de la population générale, résultat qui a été trouvé tant avant qu'après avoir tenu compte de l'effort réduit pour obtenir des photographies vers le début et vers la fin de la période de migration. Par conséquent, certaines parties du centre de la mer de Beaufort où l'eau atteint une profondeur allant jusqu'à 200 m semblent plus utilisées par les baleines boréales immatures que par les baleines adultes pendant la plupart des années. Par ailleurs, il existait une variation interannuelle importante sur le plan de la répartition des fréquences de longueur des baleines en fonction des années, des subdivisions géographiques de la région à l'étude, des catégories de profondeur de l'eau et des périodes. Cette variation était attribuable à l'utilisation variable de la région visée par l'étude par chaque classe de dimension au cours des différentes années, aux différences de profondeur de l'eau utilisée par les différentes classes de dimension ainsi qu'aux périodes de migration différentes de chaque classe de dimension. Dans le cas de toutes les années, les petites baleines immatures dominaient les habitats peu profonds (< 20 m) en zone côtière, et la taille des baleines augmentait en fonction de la profondeur de l'eau. Le moment des déplacements vers la région à l'étude et dans celle-ci dépendait également de la classe de dimension : les petites baleines immatures arrivaient en premier, vers la fin août et repartaient vers la fin septembre, tandis que les baleines adultes arrivaient en dernier, vers la fin septembre. Les mères et leurs baleineaux arrivaient au début septembre et y restaient au moins jusqu'au début octobre.

Mots clés : baleine boréale, *Balaena mysticetus*, utilisation de l'habitat, photogrammétrie, longueurs, alimentation, migration

[1] LGL Ltd., environmental research associates, 22 Fisher St., P.O. Box 280, King City, Ontario L7B 1A6, Canada; bkoski@lgl.com
[2] Deceased
© The Arctic Institute of North America

automnale, profondeur de l'eau, date, variation annuelle, productivité

Traduit pour la revue *Arctic* par Nicole Giguère.

INTRODUCTION

Habitat segregation of different size classes of bowhead whales (*Balaena mysticetus*) in the Bering–Chukchi–Beaufort (BCB) population has been documented in summering areas in the eastern (i.e., Canadian) and central Beaufort Sea and in Amundsen Gulf (Cubbage and Calambokidis, 1987; Koski et al., 1988). Those studies, and observations by local residents (Galginaitis and Koski, 2002), indicate that small subadult whales tend to occupy shallow nearshore areas along the Yukon and eastern Alaskan coasts. Large subadults tend to be found farther offshore along those coasts and in shallow waters farther east (i.e., north of the Mackenzie Delta and the Tuktoyaktuk Peninsula). Adults tend to be found even farther east. Bowheads found in Amundsen Gulf are almost exclusively adults (Koski et al., 1988).

Temporal, as well as spatial, segregation by size class has been seen in parts of the BCB bowhead range. Whalers from Kaktovik, along the coast of the central Beaufort Sea, have stated that in late summer, small bowheads arrive in nearshore waters near Kaktovik earlier than larger whales, but that all sizes of whales are seen near Kaktovik over the autumn season (Braham et al., 1984; Galginaitis and Koski, 2002). However, harvest data from Kaktovik do not show any seasonal trend in the proportion of small whales harvested, presumably because whalers selectively harvest small whales (Koski et al., 2005). Temporal segregation also occurs during spring migration past Barrow (Zeh et al., 1993; Angliss et al., 1995; Koski et al., 2006). A large proportion of the whales passing Barrow early in the spring migration period are subadults, and a large proportion of those passing near the end of the period are adults. Females accompanied by recently born calves are among the last whales to pass Barrow in spring (Angliss et al., 1995; Koski et al., 2006).

For the Baffin Bay–Hudson Bay bowhead stock, there is also evidence that in summer, different components of the stocks concentrate in different parts of their overall ranges (Finley, 1990, 2001; Cosens and Blouw, 2003).

In some years, the central Beaufort Sea may be an important feeding area for some individual bowhead whales during late summer and autumn (Lowry, 1993; Lowry et al., 2004). At this time of year bowheads commence their westward migration to overwintering areas (Moore and Reeves, 1993; Mate et al., 2000; Koski et al., 2005), either stopping to feed at times or feeding while traveling (Würsig et al., 2002).

This study examines bowhead size data collected in the central Beaufort Sea during late August through early October of 1982, 1984 to 1986, and 1998 to 2000 in relation to year, location within the study area, water depth, and date. It assesses the size classes of bowhead whales found in this area and evaluates whether there was habitat or seasonal segregation (or both) by size class (small subadults vs. large subadults vs. adults) and status (mothers vs. other adults). This information is needed to correct aerial survey data for size-related variation in detectability in different regions and at different times of the late summer–fall period. It is also relevant in evaluating the importance to the different components of the bowhead whale population of specific parts of the study area that may be developed by the oil and gas industry. In addition, a traditional bowhead hunt occurs near Kaktovik, and interactions among the proposed developments, the traditional harvest, and future changes in bowhead use of different parts of the central Beaufort Sea may need to be evaluated. Also, recent studies have found a relationship between sea-ice cover and bowhead whale distribution (Moore et al., 2000; Treacy et al., 2006), so reductions in summer and autumn sea-ice cover due to global warming may result in changes to bowhead distribution. Finally, the bowhead whale population is increasing (George et al., 2004; Zeh and Punt, 2005) and includes a high proportion of immature animals (Angliss et al., 1995; Koski et al., 2006). Thus, it is important to document the sizes of bowhead whales in relation to any past or future changes in their use of the central Beaufort Sea.

Methods

The study area consisted of the central Beaufort Sea from Flaxman Island, Alaska (146˚ W) almost to Herschel Island, Yukon (139˚ W), between the coast and 71˚ N (Fig. 1). Our study area includes the eastern two-thirds of the U.S. Minerals Management Service (MMS) Eastern Region (Treacy, 2000). Almost all of the available data came from areas with waters no deeper than 200 m.

Data Sources

Length measurements used here were obtained by photogrammetry conducted during numerous studies during late August to early October in seven years from 1982 to 2000 (Table 1). Most of the data presented here came from studies funded by the MMS in 1985–86 and 1998–2000.

Bathymetry data were obtained from the U.S. National Oceanic and Atmospheric Administration and included Hydrographic Survey Data Volume 1, version 3.1, and Marine Geophysical Data/Bathymetry, Magnetics, Gravity, version 3.2. Point soundings and gridded bathymetry data were contoured using a triangulated irregular network (TIN) algorithm in the Vertical Mapper add-on module for MapInfo Professional. Depths at sites of whale sightings were interpolated from the sounding data and contour lines.

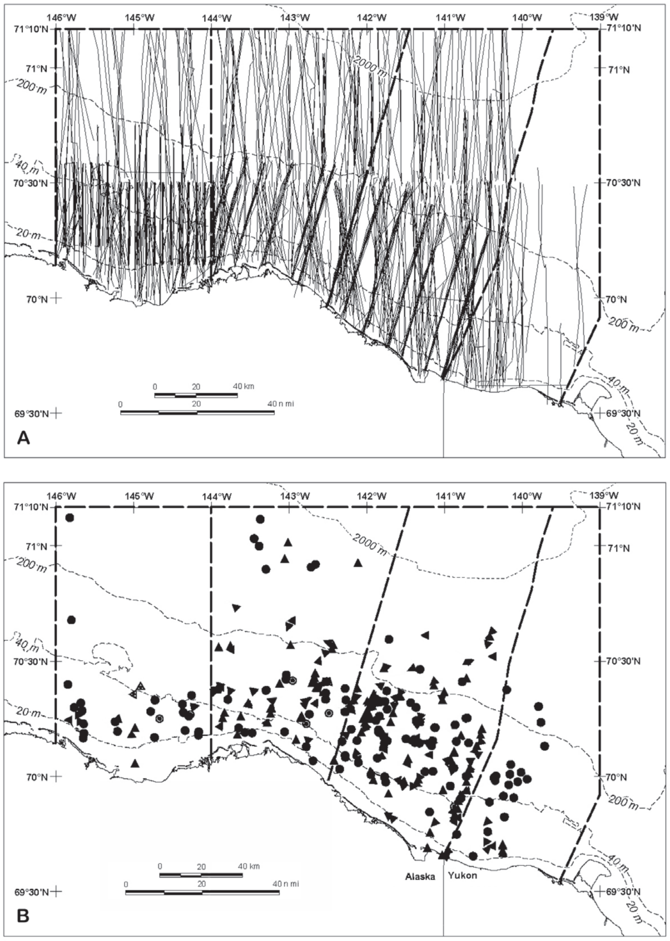

FIG. 1. (A) Systematic aerial survey effort and (B) bowhead whale sightings during the periods shown in Table 1 when bowhead whale photographs were taken. Symbols represent sightings during surveys by LGL (triangles) and MMS (circles).

Effort to Obtain Photographs

Many of the data presented here were obtained during a study of the importance of the central Beaufort Sea to bowhead whales (Richardson and Thomson, 2002). On three to six occasions during each year in 1985–86 and 1998–2000, we, the MMS, or their contractors (Treacy, 2000) conducted a systematic survey of the entire study area (Fig. 1A) to determine the distribution of bowheads (Fig. 1B). Miller et al. (2002) show more details of the effort and whale sightings during these systematic surveys.

On other days with suitable weather, we conducted "search surveys" to find bowhead whales in order to observe their behaviour and photograph them. The choice of tracks for our search surveys and the resulting photography sessions was guided by our knowledge of whale distribution acquired from the systematic surveys; however, not every flight resulted in whale sightings (Table 1). Whenever whales were sighted, effort to find whales stopped, and either photography or another research activity was initiated. Thus, effort to find whales to photograph was lowest during 1999, when whales were abundant in the study area, and highest during 2000, when whales were scarce. Photographs were more likely to be obtained at locations where whales lingered and were less likely to be obtained when whales migrated steadily through the study area.

Photogrammetry

We used the calibrated vertical photography technique developed by LGL (Koski et al., 1992, 2006). Briefly, the aircraft flew at an airspeed of ~160 km/h and an altitude of ~137 m (450 ft, cloud ceiling permitting) and passed directly over bowheads. Photographs were taken through the aircraft's ventral camera port with one of two hand-held Pentax medium-format cameras (6×7 cm film size), each with a 105 mm f 2.4 lens, pointed directly downward. Shutter speed was 1/500 second or, when possible, 1/1000 second. We used Kodak Ektachrome 200 or 400, or Fujichrome Provia 400, which are color positive films, or occasionally (in 1985) Ilford XP1 black-and-white negative film pushed to ISO (ASA) 1600. Aircraft altitude was read manually from the radar altimeter's analog display or from a digital readout (or both) at the moment the camera shutter tripped and was recorded on data sheets. Calibration targets of known dimensions were deployed one to three times each season and photographed with each of the cameras used during that season. These photos were taken from the same altitudes that were flown during whale photography sessions. Whale images and calibration targets were measured using a stereo microscope and stage micrometer, as described by Koski et al. (1992, 2006). The measured image sizes were converted to whale lengths, accounting for systematic biases introduced by the cameras (focal plane shutter distortion or inaccurate nominal lens length) and by biases in the output from the radar altimeter.

The resulting length measurements varied in reliability depending on the circumstances during photography, the position of the whale relative to the water surface, and the quality of the whale image. Length data categorized as "accurate" (grades 1–6 of Koski et al., 1992) were generally accurate to within a few decimeters (Koski et al., 2006). Length data categorized as "approximate" were obtained by estimating whale length from measurements of fluke width or snout-to-blowhole distance, or from photos taken when the aircraft altitude was changing rapidly; "approximate" lengths were generally accurate to within ~1 m. Both "accurate" and "approximate" length data were used in assessing size distributions of whales within the study area, but only "accurate" lengths (i.e., grades 1–6 of Koski et al., 1992) were used in describing life history information (Koski et al., 1993, 2006).

All images with potential to be re-identified were printed and compared with one another to check for whales photographed more than once within each field season. These procedures were summarized by Rugh et al. (1992, 1998). When a whale was photographed more than once in a given year and season (considering summer and early autumn as a single season), all "accurate" length measurements were

TABLE 1. Sources of bowhead whale length measurements for this study. Additional effort and photos outside the present study area during some listed studies are not included.

Year	Days with Flights	Photo Sessions	Measured Whales	Date Range of Photos	Study Sponsor	Source of Data
1982	3	3	11	16 August – 4 September	National Marine Fisheries Service	Davis et al., 1983
1984	4	4	34	17 August – 14 September	Indian & Northern Affairs Canada	Davis et al., 1986a
1985	8	10	123[1]	11 – 29 September	U.S. Minerals Management Service	Richardson, 1987
1985	2	4	60[1]	28 August – 8 September	Sohio Alaska Petroleum et al.	Davis et al., 1986b
1985	1	1	2	19 September	Shell Western Exploration & Production Inc.	Johnson et al., 1986
1986	11	13	173[2]	3 – 7 September	U.S. Minerals Management Service	Richardson, 1987
1986	10	12	41[2]	5 September – 3 October	Shell Western Exploration & Production Inc.	Koski and Johnson, 1987
1998	8	18	111	14 – 22 September	U.S. Minerals Management Service	Richardson and Thomson, 2002
1999	12	31	329	10 – 29 September	U.S. Minerals Management Service	Richardson and Thomson, 2002
2000	6	9	27	13 – 21 September	U.S. Minerals Management Service	Richardson and Thomson, 2002
Total	65	105	901[1,2]	16 August – 3 October		

[1] Five whales were photographed during two 1985 studies, so only 180 different whales were measured in 1985.
[2] Five whales were photographed during both 1986 studies, so only 209 different whales were measured in 1986.

averaged to obtain a "best length" (Koski et al., 2006). Only a single measurement is presented for each whale for each period or for each geographic zone (Fig. 2) where it was photographed, regardless of the number of times that whale was photographed. The sample sizes are different for the various analyses because some whales were photographed on two or three days during a year, and those whale lengths are included once in each category where they occurred. For example, a whale photographed in the Komakuk area on one day and the Camden area later in the same year would be included in the length-frequency distributions for both Komakuk and Camden, but only once in the overall length-frequency distribution for that year.

Length Categories

During late summer and early autumn, whales less than ~7 m long are generally calves less than one year old (Koski et al., 1993). Some calves may be as long as 7.5 m by September. Animals 13 m long or under were classified as subadults unless they were calves, as determined by morphology (Koski et al., 1993). Subadults were further broken down into small (< 10 m) and large (≥ 10 m) subadults. Whales over 13 m long were considered to be mature adults (Nerini et al., 1984; Koski et al., 1992, 1993), although some females with calves are as small as 12.2 m, and some females slightly longer than 13.5 m are not mature (Nerini et al., 1984; Koski et al., 1993). "Others" are all adult whales excluding mothers and calves.

Geographic and Temporal Categories

Length-frequency distributions of whales were derived for the four geographic zones or subdivisions of the study area (east to west: Komakuk, Demarcation Bay, Kaktovik, and Camden Bay; Fig. 2) and four categories of water depth: nearshore (< 20 m), middle shelf (20–40 m), shelf break (40–200 m), and continental slope (> 200 m). Length-frequency distributions of bowhead whales in the study area were examined for each year in which photographs were obtained, and for half-month periods (all years combined) from mid-August to mid-October. For each of these periods and locations, length-frequency distributions were condensed to numbers of whales in each of the five categories based on size and status. Chi-square goodness-of-fit tests were used to test for differences among half-month periods and locations in the proportions of whales in the five categories.

RESULTS

Overall Length-Frequency Distribution

A total of 901 different bowhead whales were measured in photographs obtained in the central Beaufort Sea in 1982–2000 (Fig. 3). An additional 33 photographs of some of these 901 whales were obtained during the same year as the original sighting, but in a different geographic zone, water-depth category, or half-month period. Of these, 6.2% were calves, 31.4% were small subadults, 33.3% were large subadults (64.7% subadults), and 29.1% were adults (5.7% recognizable mothers and 23.4% other adults) (Table 2).

Year-to-Year Variation

The proportions of whales of different size and status categories differed significantly among the years (1982 and 1984 were excluded because of small sample sizes) whether mothers and calves were included ($\chi^2 = 126.3$, df = 16, $p < 0.001$) or excluded ($\chi^2 = 98.9$, df = 8, $p < 0.001$) (Fig. 4). Much of this year-to-year difference was due to the considerable variation in the proportional occurrence and sizes of subadult whales photographed in the study area during different years. Survey coverage and timing of surveys were similar during 1985–86 and 1998–2000. The years 1984 (excluded from the statistical test) and 1998 had the highest proportions of small subadult whales; 1986 had nearly equal numbers of small and large subadults; and 1985 and

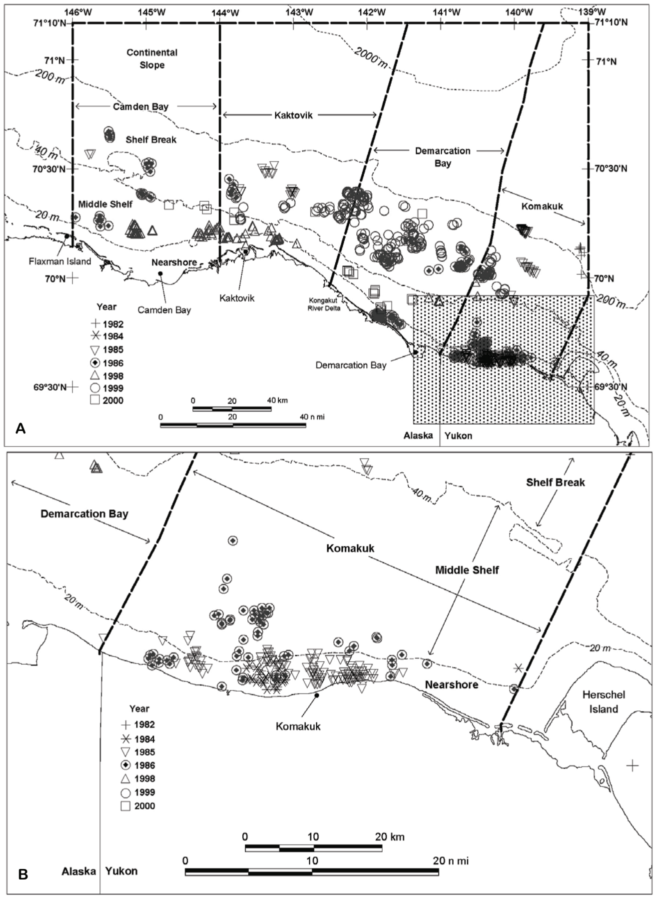

FIG. 2. (A) Map of the study area, showing its subdivision into four geographic zones (east to west: Komakuk, Demarcation Bay, Kaktovik, and Camden Bay) and the locations where individual whales were photographed to obtain length data in 1982, 1984–86, and 1998–2000. Each of the 901 whales is shown only once for each year, geographic zone, depth stratum, and half-month time period, at the location where it was first photographed. (B) Close-up of the area around Komakuk on the north coast of the Yukon, the shaded area in (A).

1999 (1982 excluded) had more large subadults than small subadults (Table 2).

There was considerable interannual variation in the percentage of measured whales that were calves ($\chi^2 = 17.45$, df = 5, $p < 0.01$; excludes small 1982 sample). Calves made up 10.5% of whales in 1986, 6.4% in 1999, and 11.1% in 2000, but only 2.2–2.9% in 1984, 1985, and 1998.

In all years except 1999, small and large subadult whales predominated among the whales measured (Fig. 4). Excluding mothers and calves, small and large subadults (combined) made up 76–100% of the measured whales in the study area during 1982–98 and 2000; in 1999, subadults made up only 52% (Table 2).

Variation by Region

The proportions of calves, small subadults, large subadults, adults excluding mothers, and mothers were significantly different among the four geographic zones of the study area ($\chi^2 = 99.97$, df = 12, $p < 0.001$). Most (81%) of the whales in the eastern part of the study area (the Komakuk

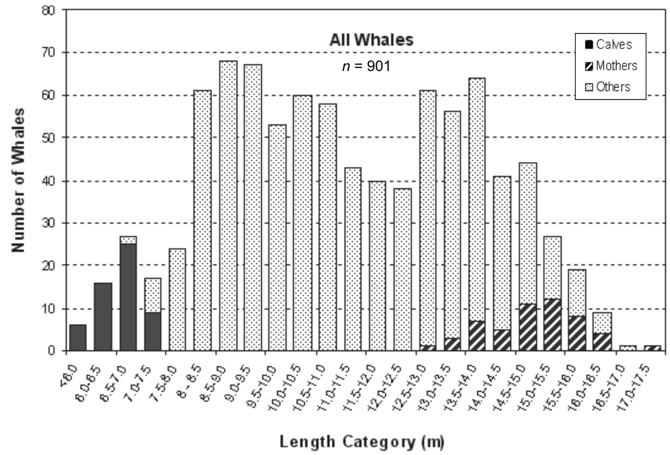

FIG. 3. Overall length-frequency distribution of bowhead whales (calves, mothers, and others) photographed in the study area in 1982, 1984–86, and 1998–2000. Duplicate measures in the same year are excluded. In the "others" category, whales up to 13 m long were considered subadults, and were classified as small (< 10 m) or large (≥ 10 m).

block) were small and large subadults (See "Others" < 13 m in Fig. 5A). Subadults also predominated in the Demarcation and Camden blocks (57% and 58%, respectively), while 33–35% of whales there were adults. Equal numbers of adults and subadults were photographed in the Kaktovik block.

Differences in the proportions of mothers and "others" in the four survey blocks were only marginally significant ($\chi^2 = 7.33$, df = 3, $p = 0.062$). There were somewhat more mothers in the Camden and Demarcation blocks (10.6% and 8.1%) than in the other blocks (4.2–4.4%).

Variation by Water Depth

The distribution by size class of bowheads changed significantly with increasing water depths ($\chi^2 = 237.57$, df = 12, $p = 0.001$). Small subadults made up 57%, 41%, and 15% of whales at water depths of less than 20 m, 20–40 m, and 40–200 m, respectively (Table 3). Adults (excluding recognizable mothers), in contrast, made up 2%, 14%, and 38% of whales in the same depth categories (Table 3, Fig. 6). The small sample of whales photographed in waters deeper than 200 m was 7% small subadults and 33% adults (excluding mothers).

The proportional occurrence of mother-calf pairs differed significantly among depth strata ($\chi^2 = 18.03$, df = 3, $p < 0.001$), primarily because mothers with calves tended to avoid waters less than 20 m deep (Fig. 6, Table 3). The proportions of mother-calf pairs were not significantly different among the three strata over 20 m deep ($\chi^2 = 2.06$, df = 2, $p = 0.357$).

The same trends for whale size to vary with water depth category that were seen in the overall length-frequency distribution were present within each geographic zone (Table 3, Fig. 7). The proportional occurrence of whales of different size classes and status was not significantly different either between the Komakuk and Demarcation blocks for water depths under 20 m ($\chi^2 = 2.67$, df = 4, $p = 0.614$)

TABLE 2. Percentages of whales in each size class within the study area, 1982–2000.

Year	1982	1984	1985	1986	1998	1999	2000	Total
All whales:								
Calves	18.2	2.9	2.2	10.5	2.7	6.4	11.1	6.2
All subadults excluding calves	63.6	94.1	83.3	66.5	81.1	45.3	59.3	64.7
Small	27.3	76.5	35.6	34.0	45.9	17.9	33.3	31.4
Large	36.4	17.6	47.8	32.5	35.1	27.4	25.9	33.3
All adults	18.2	2.9	14.4	23.0	16.2	48.3	29.6	29.1
Non-mother adults	0.0	0.0	12.2	15.8	13.5	41.3	18.5	23.4
Mothers	18.2	2.9	2.2	7.2	2.7	7.0	11.1	5.7
Number measured	11	34	180	209	111	329	27	901

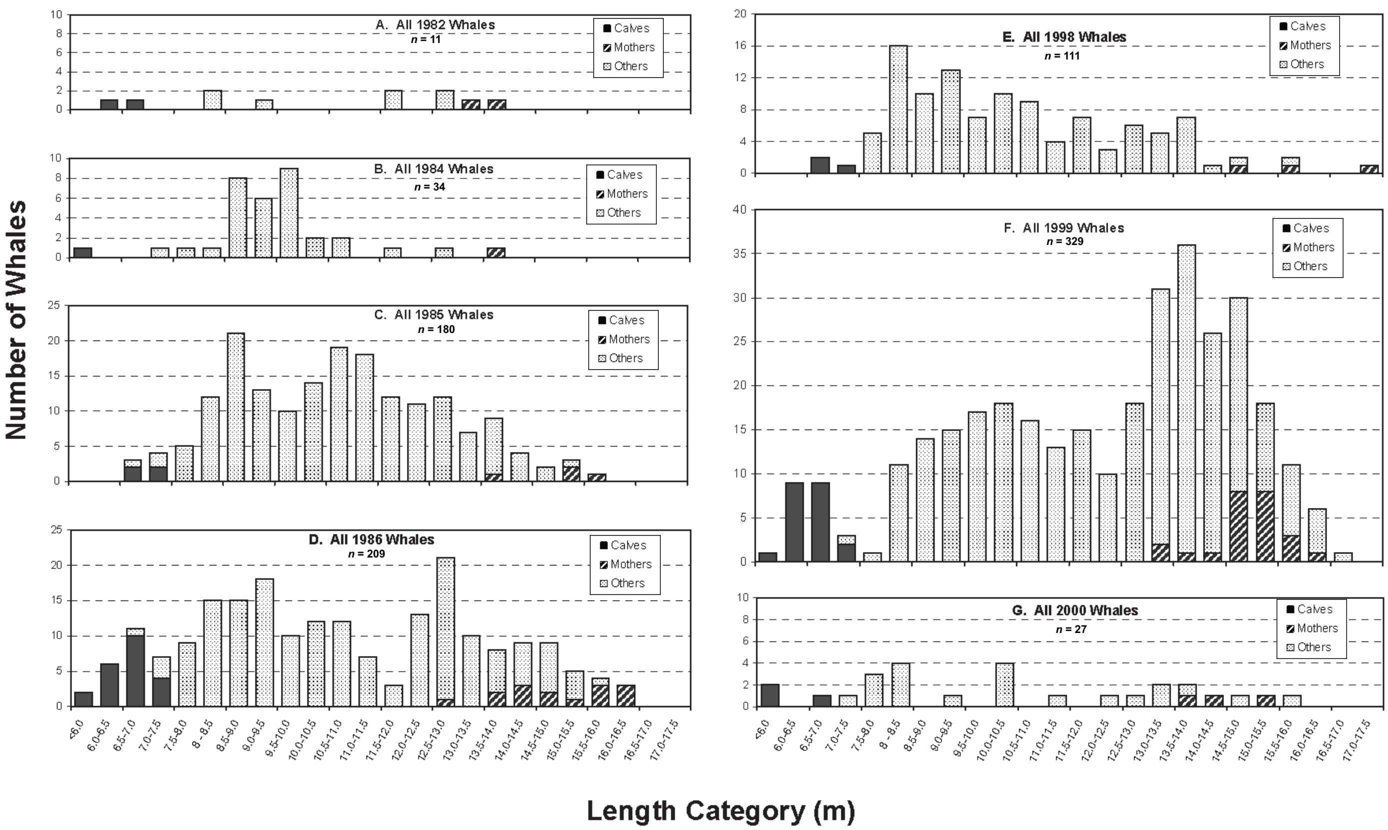

FIG. 4. Annual length-frequency distributions of bowhead whales photographed in the study area in 1982, 1984–86, and 1998–2000. Within-day and between-day repeats are excluded.

or among the four geographic zones for water depths of 20–40 m ($\chi^2 = 15.75$, df = 12, $p = 0.203$). (Zones and depth strata with fewer than 25 whales have been excluded from statistical tests because of small expected values.) However, for water depths 40–200 m, there were significant differences in whale size classes (mothers and calves excluded) among the Komakuk, Demarcation, and Kaktovik areas ($\chi^2 = 27.94$, df = 4, $p < 0.001$). This difference was due to a more pronounced shift from small to large bowheads with increasing water depth in the Kaktovik block than in the Komakuk block (Fig. 7).

Temporal Variation

There was a significant change in the size classes of bowhead whales within the central Beaufort Sea from mid-August to mid-October, the period when bowhead whales are common in that area ($\chi^2 = 94.37$, df = 12, $p < 0.001$). During 16–31 August, 93% of measured whales were subadults (small subadults + large subadults). The percentage of subadults declined to 73% during 1–15 September, 56% during 16–30 September, and 35% during 1–15 October (Fig. 8). Corresponding increases in the percentages of adults (including mothers) were observed during the four time periods (4%, 20%, 38%, and 48%).

There was also a significant seasonal difference in the proportions of recognizable mothers vs. other adults and subadults photographed during late summer and early autumn ($\chi^2 = 10.20$, df = 3, $p = 0.017$). Recognizable mothers formed 1.4%, 6.6%, 5.6%, and 17.4%, respectively, of the whales photographed in the four half-month periods from late August to early October. However, the number of

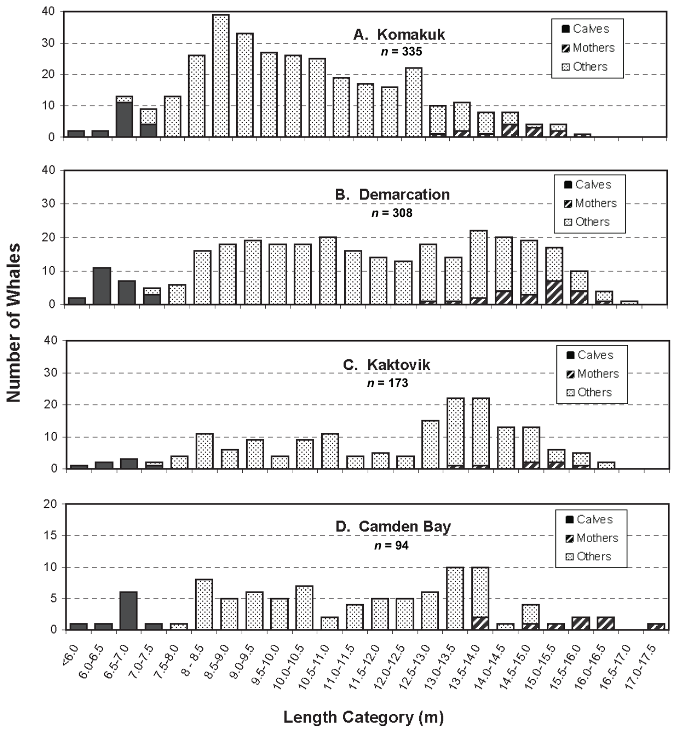

FIG. 5. Length-frequency distributions by area of bowhead whales photographed in the (A) Komakuk, (B) Demarcation, (C) Kaktovik, and (D) Camden Bay areas in 1982, 1984–86, and 1998–2000. See Figure 2 for area boundaries. Whales photographed repeatedly in the same zone or year are shown only once for each zone in each year.

whales measured in October was small (4 mothers and 15 others).

The significant increase in the sizes of whales as the season progressed was evident in two factors: a tendency for the whales in shelf-break waters (40–200 m deep) to be larger late in the season, and a tendency for the whales to be farther offshore (where larger whales predominated) late in the season (Fig. 9). In water 40–200 m deep, the proportions of whales of different size classes differed significantly between early and late September ($\chi^2 = 25.03$, df = 4, $p < 0.001$). At those depths, the proportion of adults increased progressively from late August to late September. In contrast, in water depths under 20 m, the proportions of whales of different sizes did not differ significantly with date over the late August–late September period ($\chi^2 = 4.60$, df = 6, $p = 0.80$). Similarly, in water 20–40 m deep, the proportions were not much different between early and late September ($\chi^2 = 6.54$, df = 4, $p = 0.162$). The seasonal trend in shelf-break waters, combined with a seasonal increase in the proportion of the bowheads photographed that were in those waters, were the main components of the overall seasonal increase in the sizes of the whales.

DISCUSSION

S.E. Moore and colleagues have examined the habitat use patterns of bowheads, gray whales (*Eschrichtius robustus*), and white whales (*Delphinapterus leucas*) during late summer and early autumn in the Alaskan Beaufort and Chukchi seas (Moore and DeMaster, 1998; Moore, 2000; Moore et al., 2000). Their analyses were based on systematic aerial surveys conducted by or for the MMS in 1982–91 (Moore et al., 1989; Treacy, 1992). Moore and DeMaster (1998) found that bowheads tended to select offshore waters (mean water depth 900 m) during July and August, and nearshore and shelf-break waters (mean water depth 109 m) during September and October. Further analyses found that bowheads tended to select nearshore waters during light and moderate ice conditions and slope waters during heavy ice conditions (Moore, 2000; Moore et al., 2000), and this tendency has persisted to recent years (Treacy et al., 2006; Blackwell et al., 2007).

Miller et al. (2002) examined bowhead habitat use in our specific study area (Moore et al. considered the entire Alaskan Beaufort and Chukchi seas) but over a longer time period (1979–2000 vs. 1982–91). Miller et al. (2002) also used additional sources of survey data, from the Richardson and Thomson (2002) study and some industry-funded studies. When whale densities were averaged over the August–October season for each water depth, the highest mean densities were in the shelf-break area (depths 40–200 m), and lowest, over the continental slope (depth > 200 m). In August, however, the highest densities were over the continental slope. When bowhead densities were averaged for the entire study area during each half-month period, the highest densities occurred during the second half of September. When averaged for each geographic zone over the season, the highest densities were in the Komakuk zone (Miller et al., 2002). Average densities of whales gradually declined from east (Komakuk zone) to west (Camden Bay zone).

However, the studies mentioned above did not include information on the sizes or activities of the whales seen during their surveys. The apparent seasonal change in habitat use may have resulted, in part, from differences in the movement patterns of different components of the population, or from changes in their behaviour that might have affected their detectability. Additional insight into bowhead whale use of the central Beaufort Sea can be obtained by integrating our findings on size class and seasonal segregation, as well as data on activities of whales of different size classes (Würsig et al., 2002), with the findings of Moore (2000), Moore et al. (2000), and Miller et al. (2002) on overall seasonal distribution.

Most of the BCB bowhead whale population is believed to migrate west through the central Beaufort Sea from summering areas in the Canadian Beaufort Sea and Amundsen Gulf to overwintering areas in the Bering Sea (Moore and Reeves, 1993). Bowheads feed within the present study area during this migration (Lowry et al., 2004), but the amount of feeding varies from year to year (Richardson and Thomson, 2002). Our data indicate that in all years, during late summer and autumn, subadult bowheads move primarily through shallow nearshore waters and adults move primarily through deeper waters. This size segregation has also

TABLE 3. Numbers and percentages (in parentheses), by water depth category and geographic zone, of whales of various size classes in the central Beaufort Sea 1982–2000. Whales photographed more than once during the same year in a given water depth category or geographic zone are counted only once.

Zone		Subadults		Adults			Overall
Water Depth	Calves	Small (< 10 m)	Large (10 – 13 m)	Mothers	Others	Total	Total
Komakuk							
< 20 m	3 (2)	102 (55)	77 (41)	1 (1)	4 (2)	5 (3)	187
20 – 40 m	2 (4)	27 (52)	18 (35)	1 (2)	4 (8)	5 (10)	52
40 – 200 m	13 (18)	15 (21)	19 (26)	10 (14)	15 (21)	25 (35)	72
> 200 m	1 (3)	2 (7)	15 (50)	2 (7)	10 (33)	12 (40)	30
Demarcation							
< 20 m	1 (3)	21 (57)	14 (38)	1 (3)	0 (0)	1 (3)	37
20 – 40 m	1 (3)	13 (43)	11 (37)	1 (3)	4 (13)	5 (17)	30
40 – 200 m	21 (9)	45 (19)	73 (30)	21 (9)	81 (34)	102 (42)	241
> 200 m	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
Kaktovik							
< 20 m	0 (0)	15 (88)	2 (12)	0 (0)	0 (0)	0 (0)	17
20 – 40 m	0 (0)	13 (45)	12 (41)	1 (3)	3 (10)	4 (14)	29
40 – 200 m	7 (6)	7 (6)	34 (27)	6 (5)	73 (57)	79 (62)	127
> 200 m	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
Camden							
< 20 m	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
20 – 40 m	7 (9)	24 (31)	24 (31)	7 (9)	15 (19)	22 (29)	77
40 – 200 m	2 (12)	1 (6)	5 (29)	2 (12)	7 (41)	9 (53)	17
> 200 m	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
All Areas							
< 20 m	4 (2)	137 (57)	93 (39)	2 (1)	4 (2)	6 (3)	240
20 – 40 m	10 (5)	77 (41)	65 (35)	10 (5)	26 (14)	36 (19)	188
40 – 200 m	42 (9)	68 (15)	131 (29)	37 (8)	172 (38)	209 (46)	450
> 200 m	1 (3)	2 (7)	15 (50)	2 (7)	10 (33)	12 (40)	30

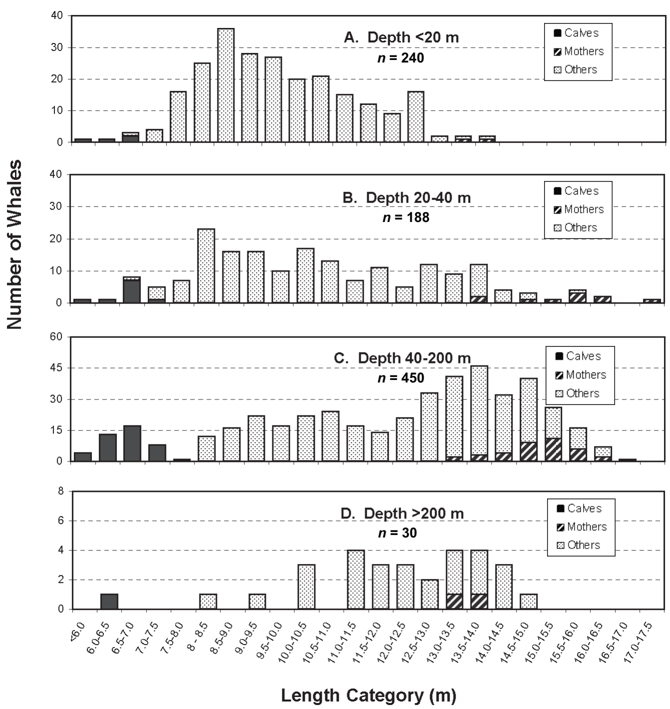

FIG. 6. Length-frequency distributions of bowhead whales photographed in various depths of water in 1982, 1984–86, and 1998–2000. Within-day and between-day repeats are excluded.

been noted by subsistence whalers at Kaktovik (Galginaitis and Koski, 2002; Koski et al., 2005). The apparent preference for shallow nearshore waters during years with light and moderate ice conditions may, at least in part, reflect more extensive feeding in these nearshore waters by subadult whales during light ice years rather than a shift in distribution from offshore to nearshore waters. No ice was present in our study area during the study periods in 1986 and 1998–2000, but even in those years most adult whales moved west through deeper waters (i.e., they were not photographed in shallow waters where primarily subadults were photographed).

Most if not all bowheads that summer in the Canadian Beaufort Sea and Amundsen Gulf migrate west through the central Beaufort Sea. They migrate at a wide range of distances from shore during their passage from Canadian summering areas to overwintering areas in the Bering Sea (Moore and Reeves, 1993). If all segments of this bowhead population make equal use of the study area, the whales photographed during our study should reflect the length-frequency distribution of the population. The overall population was estimated to include 5.2% calves, 53.7% subadults, and 41.1% adults during 1985–92, based on 1898 whales photographed during the spring migration past Point Barrow and corrections to the length-frequency distribution for periods without photographic effort (Angliss et al., 1995). Proportionally more subadults and fewer adults were photographed in the central Beaufort Sea than reported by Angliss et al. (1995) ($\chi^2 = 31.61$, df = 2, $p < 0.001$). The proportion of bowheads photographed in the study area that were calves was not significantly different than in the results of Angliss et al. (1995) ($\chi^2 = 0.93$, $p = 0.335$).

Our sample is biased because our photographic surveys did not include all of the late summer–early autumn

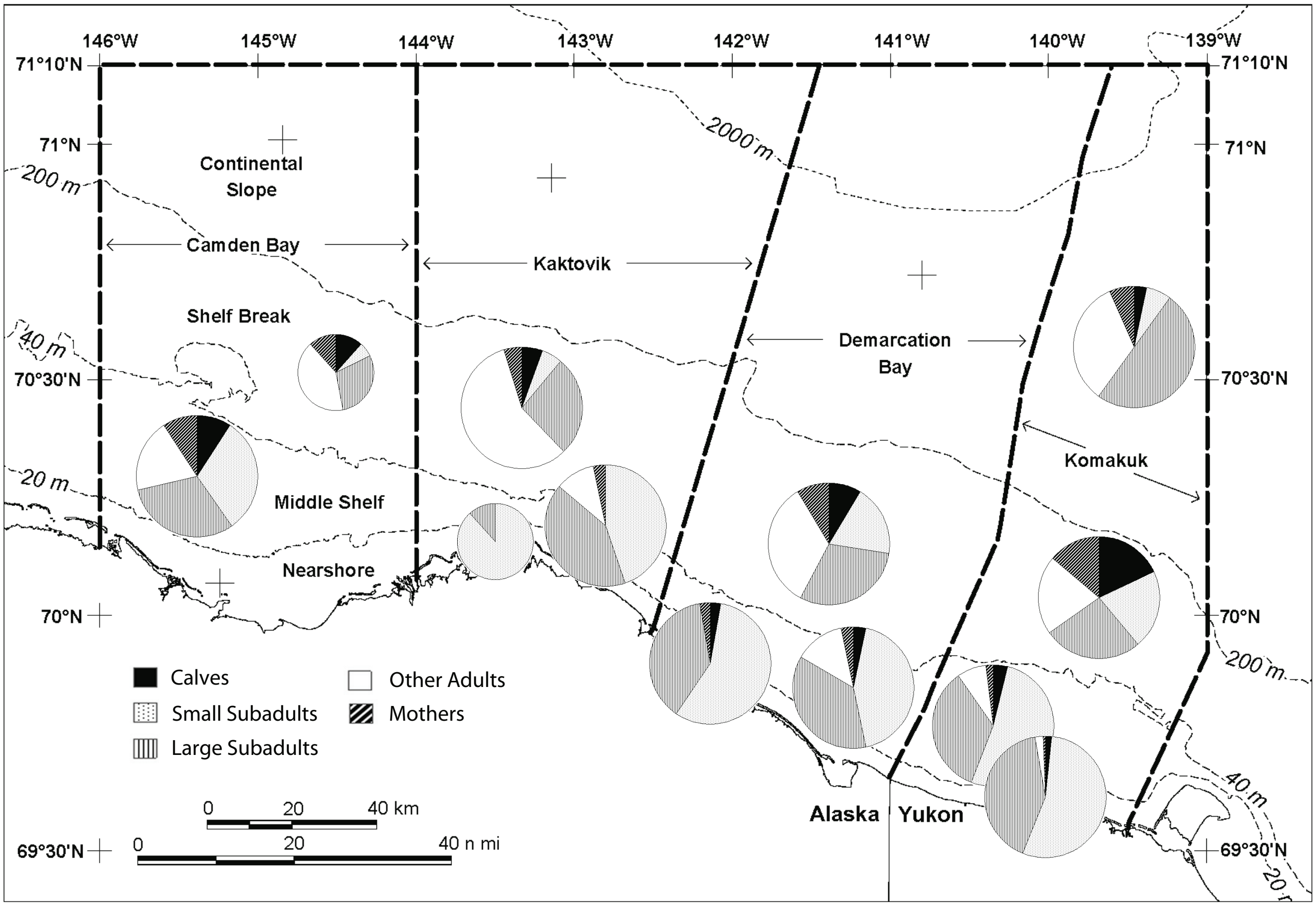

FIG. 7. Pie charts showing proportions of whales of various size classes in the central Beaufort Sea, by water depth category and geographic zone, in 1982, 1984–86, and 1998–2000. Large pie-charts represent more than 25 different measured whales, and small charts, 15–25 whales. No charts are shown for areas with fewer than 15 whales.

migration period. Although residents of Kaktovik have noted that in some years bowheads are seen near Kaktovik as early as July and as late as late October (Galginaitis and Koski, 2002; Koski et al., 2005), most bowheads pass Kaktovik from late August to mid-October (Miller et al., 2002). We acquired some length data on dates ranging from 16 August to 3 October. However, during the primary years of this study (1985–86 and 1998–2000), the average dates when our photographic work began and ended were 8 and 27 September (Table 1). Data on the timing of the bowhead migration in our study area from Richardson and Thomson (2002: Appendix 9.1) indicate that, in an average year, 20% of the migration has entered our study area during the period from 26 August through 7 September, and 29% of the migration enters the study area after 27 September. Fourteen percent of our photographs were obtained before 8 September and 10% were obtained after 27 September (Table 4A). If we correct our photographic sample to account for the under-sampling during the early and late periods, the percentage of subadults declines from 64.7% to 61.3%, and the percentage of adults increases from 29.2% to 32.6% (Table 4B). Thus, the corrected percentage of adults (32.6%) passing through our study area is still much lower than the 41.1% adults in the spring data of Angliss et al. (1995) or the 39.8% adults estimated to be in the population by Koski et al. (2006). Those additional adults may have migrated north of our study area or later in the season than surveys were conducted.

Prey availability affects the distribution of bowheads during late summer and early autumn (Bradstreet and Fissel, 1987; Bradstreet et al., 1987; Moore et al., 1995; Richardson and Thomson, 2002). Bowheads aggregate and linger in areas where food is abundant. Feeding was the most frequently observed activity of bowheads in the central Beaufort Sea during September of most years (Würsig et al., 2002). About 83% of the bowheads harvested there had food in their stomachs, with ~39% containing a substantial amount of food when landed (Lowry et al., 2004). Thus, the overall higher proportion of subadults among the measured whales suggests that the central Beaufort Sea was more important as a feeding area for subadult bowheads than for adults during the years of our study. However, the deeper waters of the central Beaufort Sea are important as an autumn migration corridor for adult whales in all years,

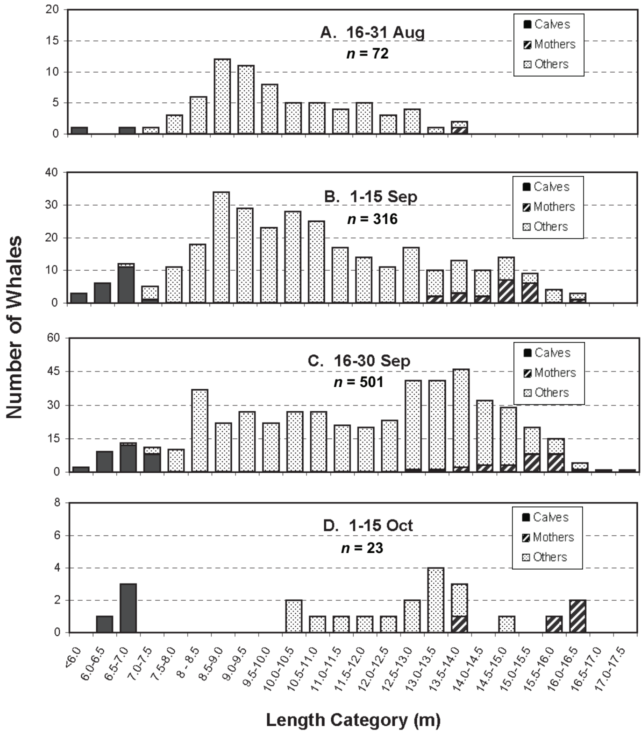

FIG. 8. Length-frequency distributions of bowhead whales photographed during four half-month periods in 1982, 1984–86, and 1998–2000. Within-day and between-day repeats are excluded.

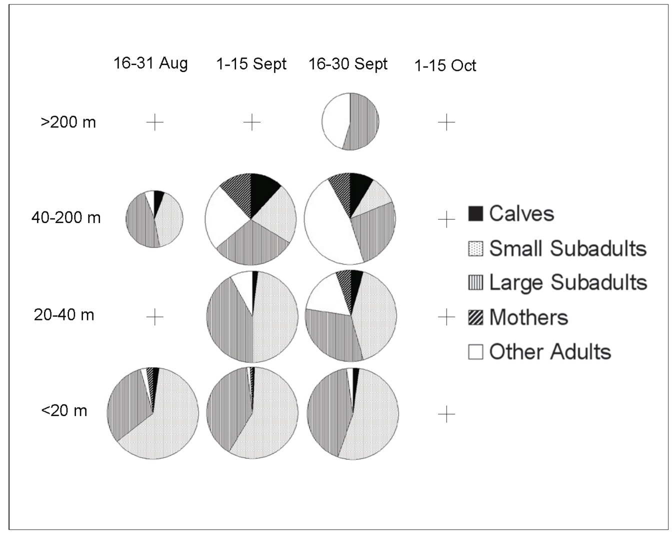

FIG. 9. Proportions of whales of various size classes by water depth category during each half-month period in the central Beaufort Sea, 1982, 1984–86, and 1998–2000. Large pie-charts represent more than 25 different measured whales, and small charts, 15–25 whales. No charts are shown for situations with fewer than 15 whales.

and they are important feeding areas in some years. In 1999, for example, adult bowheads in waters deeper than 20 m spent an estimated 66% of their time in the study area feeding (Würsig et al., 2002). Stomach-content data from bowheads harvested at Kaktovik show that most adults, as well as most subadults, had been feeding in the area (Lowry et al., 2004).

Several factors not included in our analysis could have influenced our ability to photograph or recognize whales. These include differential detection due to size-related differences in diving behaviour (Angliss et al., 1995; Koski et al., 2006) and bias in our size class distributions due to size-related differences in detection of duplicate sightings (Angliss et al., 1995; Koski et al., 2006). The distributions of the photographed whales could also have been affected by other factors known to influence whale distribution, including sea ice (Treacy et al., 2006) and industrial activities (Richardson et al., 1995). However, these factors should not have had any significant effects on our analyses or conclusions because we compared length-frequency distributions of whales, not their absolute numbers, among time periods, water depth categories, and geographic zones. Any bias in the length-frequency distributions should be similar in all categories compared. The method of photographing whales minimized bias associated with differential detection of whales because we remained with each group until most or all were photographed, and the relatively short period of the study each year minimized loss of the short-term identifying marks that were used to match whale photographs. Ice conditions or industrial activity differed among years, but sizes of whales using different locations and water depths were consistent among years. Thus, any bias that existed must have been minor in comparison to the observed differences in size class among locations, water depth categories, and date.

The substantial year-to-year variation in the proportions of adult, large subadult, and small subadult bowheads in the eastern Alaska Beaufort Sea indicates that different segments of the population lingered in the area for different periods in different years. In some years, most notably 2000, few bowheads of any size category were photographed despite considerable effort to obtain photographs. This and other evidence indicates that no segment of the population lingered in the study area in September 2000 (Richardson and Thomson, 2002).

There was considerable among-year variation in the geographic zones where bowheads were seen and photographed. This was probably related to the local abundance of bowhead prey and the differing locations of water mass boundaries that affect zooplankton (Griffiths et al., 2002). Similar among-year variation in bowhead distribution has been documented in summering areas in the Canadian Beaufort Sea (Richardson et al., 1987; Moore and Reeves, 1993).

Data from systematic aerial surveys suggest that more bowheads used the present study area in the 1990s than in the 1980s (Miller et al., 2002). Whether there has been a corresponding change in use of different parts of the study area by different size classes of bowhead whales is uncertain, given the few years with intensive photographic work and the large interannual variation. However, in the mid-1980s, subadult bowheads frequently concentrated in shallow nearshore waters in the eastern part of our study area from the Kongakut River Delta to Herschel Island, and lingered in those areas for periods of days to a few weeks

TABLE 4. Numbers and percentages of whales of various size classes (A) photographed during three time periods during this study and (B) corrected for seasonal bias in sampling effort, using aerial survey data from Richardson and Thomson (2002: Appendix 9.1). In (B), italicized values are the numbers that would be expected if effort early and late in the season had been comparable to effort during 8–27 September.

		Subadults		Adults				
	Calves	Small (< 10 m)	Large (10–13 m)	Mothers	Others	Total	All Whales	% of Whales
A: Photographed								
Before 8 September	4	67	46	4	2	6	123	13.6
8 – 27 September	46	211	227	41	167	208	692	76.7
After 27 September	6	5	27	6	43	49	87	9.6
Total	56	283	300	51	212	263	902[1]	100.0
% of whales	6.2	31.4	33.3	5.7	23.5	29.2	100.0	
B: Corrected for Sampling Effort								
Before 8 September	*9*	*148*	*101*	*9*	*4*	*13*	*271*	20.0
8 – 27 September	46	211	227	41	167	208	692	51.0
After 27 September	*27*	*23*	*122*	*27*	*194*	*222*	*393*	29.0
Total	82	381	451	77	366	443	1357	100.0
% of whales	6.0	28.1	33.2	5.7	27.0	32.6	100.0	

[1] One whale was photographed on 27 September and 1 October.

(Richardson et al., 1987). High concentrations of zooplankton, especially the small copepod *Limnocalanus macrurus*, were often found in nearshore waters during those years. In contrast, few bowheads were recorded there in 1998–2000, and those that were recorded there did not appear to linger. *Limnocalanus* was absent or scarce in nearshore waters of the study area in 1998–2000 (Griffiths and Thomson, 2002; Griffiths et al., 2002).

Large numbers of subadult bowheads have been recorded in shallow nearshore waters along the Yukon Coast and off the Tuktoyaktuk Peninsula during summer and early autumn in some years (Davis et al., 1986b; Moore and Reeves, 1993). Subadults are probably attracted to these areas by abundant food resources (Bradstreet and Fissel, 1987; Bradstreet et al., 1987; Griffiths et al., 2002). Subadult bowheads may concentrate in shallow nearshore areas because they are not physiologically well-adapted to feeding in deep offshore waters. Their dive durations tend to be shorter than those of adult whales (Richardson et al., 1995; Thomas et al., 2002). In deep water, subadults may not be able to spend enough time at depths where food organisms are abundant to feed efficiently. The shorter baleen of subadults and the consequent effects on feeding efficiency may be factors as well.

There was segregation among whales of different size classes in the timing of migration into and through the study area. Small subadult whales arrived in the study area, especially the nearshore zone, in late August and early September (Fig. 9). They were still present during late September, but were scarce or perhaps absent by early October. Large subadults and mothers with calves became common in early September, and other adults arrived mainly in late September and early October. The tendency for progressively larger whales to move through the area later in the season is similar to the pattern of the spring migration (Zeh et al., 1993; Angliss et al., 1995; Koski et al., 2006). However, the pattern for mothers and calves is different in spring and autumn. During spring, mothers and calves (excluding yearlings) are the last segment of the population to pass Barrow (Angliss et al., 1995; Koski et al. 2006). In contrast, during late summer and autumn, mothers and calves started to arrive in the central Beaufort Sea rather early in the migration period (early September), when subadult whales were the predominant animals present. Mothers and calves were also among the whales present in the study area during early October.

Although mothers and calves tended to avoid shallow nearshore areas, they were more evenly dispersed in the remainder of the study area than were other whales. Proportions of mothers and calves were generally similar in all four geographic zones and in all three water depth classes greater than 20 m, even though the proportions of subadults and adults varied markedly among those same zones and depths.

The size, spatial, and temporal segregation of bowhead whales documented during this study indicate the importance of collecting information on the sizes of whales present during surveys. The size information is useful in interpreting survey results and important to consider when comparing results among surveys. Failure to account for changes in the sizes of whales over the migration period and the differing habitat preferences of different sizes of whales can lead to misinterpretation of the reason for apparent changes in distribution. This consideration is important when trying to assess the effects of industrial activities or habitat variables, such as ice cover, on whale distribution.

ACKNOWLEDGEMENTS

We thank the numerous LGL personnel, aircraft charter companies, and pilots who assisted in collecting the photogrammetry data over the years. We thank W.J. Richardson and R.A. Davis for guidance during the many studies that provided data for this paper and W.J. Richardson, Sue Moore, and anonymous reviewers for reviewing it. The U.S. Minerals Management Service, Alaska OCS Region, sponsored the 1998–2000 work, the majority of the 1985–86 work, and this analysis. Other studies in the 1980s, as listed in Table 1, were sponsored by Shell Western Exploration & Production Inc., the U.S. National Marine Mammal Laboratory (Seattle, WA), the Canadian Department of Indian Affairs & Northern Development, and a consortium organized by Sohio Alaska Petroleum Co. (now BP). Projects in Alaska were conducted under the provisions of Scientific Research Permits 517, 518, and 481–1464 issued by the National Marine Fisheries Service. Projects in Canada were authorized under permits issued by Canadian Department of Fisheries and Oceans and in consultation with the Inuvialuit.

REFERENCES

Angliss, R.P., Rugh, D.J., Withrow, D.E., and Hobbs, R.C. 1995. Evaluations of aerial photogrammetric length measurements of the Bering-Chukchi-Beaufort seas stock of bowhead whales (*Balaena mysticetus*). Report of the International Whaling Commission 45:313–324.

Blackwell, S.B., Richardson, W.J., Green, C.R., Jr., and Streever, B. 2007. Bowhead whale (*Balaena mysticetus*) migration and calling behavior in the Alaskan Beaufort Sea, autumn 2001–04: An acoustic localization study. Arctic 60(3):255–270.

Bradstreet, M.S.W., and Fissel, D.B. 1987. Zooplankton of a bowhead whale feeding area off the Yukon coast in August 1985, Part 2. In: Bowhead whale food availability characteristics in the southern Beaufort Sea: 1985 and 1986. Environmental Studies 50. Ottawa: Indian and Northern Affairs Canada. 155 p.

Bradstreet, M.S.W., Thomson, D.H., and Fissel, D.B. 1987. Zooplankton and bowhead whale feeding in the Canadian Beaufort Sea, 1986, Part 1. In: Bowhead whale food availability characteristics in the southern Beaufort Sea: 1985 and 1986. Environmental Studies 50. Ottawa: Indian and Northern Affairs Canada. 204 p.

Braham, H.W., Krogman, B.D., and Carroll, G.M. 1984. Bowhead and white whale migration, distribution, and abundance in the Bering, Chukchi, and Beaufort seas, 1975–78. NOAA Technical Report NMFS SSRF-778, NTIS PB84-157908. Seattle, Washington: National Oceanic & Atmospheric Administration, National Marine Fisheries Service. 39 p.

Cosens, S.E., and Blouw, A. 2003. Size- and age-class segregation of bowhead whales summering in northern Foxe Basin: A photogrammetric analysis. Marine Mammal Science 19(2):284–296.

Cubbage, J.C., and Calambokidis, J. 1987. Size-class segregation of bowhead whales discerned through aerial stereophotogrammetry. Marine Mammal Science 3(2): 179–185.

Davis, R.A., Koski, W.R., and Miller, G.W. 1983. Preliminary assessment of the length-frequency distribution and gross annual recruitment rate of the Western Arctic bowhead whale as determined with low-level aerial photography, with comments on life history. Report from LGL Limited, Toronto, Ontario, for U.S. National Marine Mammal Laboratory, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, Washington 98115-0070. Paper SC/35/PS5 presented to the IWC Scientific Committee, June 1983. 91 p.

———. 1986a. Experimental use of aerial photogrammetry to assess the long term responses of bowhead whales to offshore industrial activities in the Canadian Beaufort Sea, 1984. Environmental Studies 44. Ottawa: Indian and Northern Affairs Canada. 157 p.

Davis, R.A., Koski, W.R., Miller, G.W., McLaren, P.L., and Evans, C.R. 1986b. Reproduction in the bowhead whale, summer 1985. Report from LGL Limited, King City, Ontario, for Standard Alaska Production Company (now BP Exploration Alaska Inc., Anchorage) and others. Paper SC/38/PS2 presented to the IWC Scientific Committee, May 1986. Available from the International Whaling Commission, The Red House, 135 Station Road, Impington, Cambridge CB4 9NP, United Kingdom. 176 p.

Finley, K.J. 1990. Isabella Bay, Baffin Island: An important historical and present-day concentration area for the endangered bowhead whale (*Balaena mysticetus*) of the eastern Canadian Arctic. Arctic 43(2):137–152.

———. 2001. Natural history and conservation of the Greenland whale, or bowhead, in the Northwest Atlantic. Arctic 54(1): 55–76.

Galginaitis, M.S., and Koski, W.R. 2002. Kaktovikmiut whaling: Historical harvest and local knowledge of whale feeding behavior. 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, Chapter 2. OCS Study MMS 2002-012; LGL Report TA2196-7. Report from LGL Limited, King City, Ontario for U.S. Minerals Management Service, Anchorage, Alaska and Herndon, Virginia. 30 p.

George, J.C., Zeh, J., Suydam, R., and Clark, C. 2004. Abundance and population trend (1978–2001) of western Arctic bowhead whales surveyed near Barrow, Alaska. Marine Mammal Science 20(4):755–773.

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, Chapter 5. OCS Study MMS 2002-012; LGL Report TA2196-7. Report from LGL Limited, King City, Ontario for U.S. Minerals Management Service, Anchorage, Alaska and Herndon, Virginia. 72 p.

Griffiths, W.B., Thomson, D.H., and Bradstreet, M.S.W. 2002. Zooplankton and water masses at bowhead whale feeding locations in the eastern 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, Chapter 6. OCS Study MMS 2002-012; LGL Report TA2196-7. Report from LGL Limited, King City, Ontario for U.S. Minerals Management Service, Anchorage, Alaska and Herndon, Virginia. 44 p.

Johnson, S.R., Greene, C.R., Davis, R.A., and Richardson, W.J. 1986. Bowhead whales and underwater noise near the Sandpiper Island drillsite, Alaskan Beaufort Sea, autumn 1985. Report from LGL Limited, King City, Ontario, for Shell Western Exploration and Production Inc., Anchorage, Alaska. Available from LGL Ltd., environmental research associates, 22 Fisher St., P.O. Box 280, King City, Ontario L7B 1A6. 130 p.

Koski, W.R., and Johnson, S.R. 1987. Behavioral studies and aerial photogrammetry. In: Responses of bowhead whales to an offshore drilling operation in the Alaskan Beaufort Sea, autumn 1986, Chapter 4. Report from LGL Limited, King City, Ontario, and Greeneridge Sciences Inc., Santa Barbara, California, for Shell Western Exploration and Production Inc., Anchorage, Alaska. Available from LGL Ltd., environmental research associates, 22 Fisher St., P.O. Box 280, King City, Ontario L7B 1A6. 371 p.

Koski, W.R., Miller, G.W., and Davis, R.A. 1988. The potential effects of tanker traffic on the bowhead whale in the Beaufort Sea. Environmental Studies 58. Report from LGL Limited, King City, Ontario, for the Department of Indian Affairs and Northern Development, Hull, Quebec. NTIS MIC-90-04552. Springfield, Virginia: National Technical Information Service. 150 p.

Koski, W.R., Davis, R.A., Miller, G.W., and Withrow, D.E. 1992. Growth rates of bowhead whales as determined from low-level aerial photogrammetry. Report of the International Whaling Commission 42:491–499.

———. 1993. Reproduction. In: Burns, J.J., Montague, J.J., and Cowles, C.J., eds. The bowhead whale. Special Publication No. 2. Lawrence, Kansas: The Society for Marine Mammalogy. 239–274.

Koski, W.R., George, J.C., Sheffield, G., and Galginaitis, M.S. 2005. Subsistence harvests of bowhead whales at Kaktovik, Alaska. Journal of Cetacean Research and Management 7(1):33–38.

Koski, W.R., Rugh, D.J., Punt, A.E., and Zeh, J. 2006. An approach to minimise bias in estimation of the length-frequency distribution of bowhead whales (*Balaena mysticetus*) from aerial photogrammetric data. Journal of Cetacean Research and Management 8(1):45–54.

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 No. 2. Lawrence, Kansas: The Society for Marine Mammalogy. 201–238.

Lowry, L.F., Sheffield, G., and George, J.C. 2004. Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents 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.

Miller, G.W., Elliott, R.E., Thomas, T.A., Moulton, V.D., and Koski, W.R. 2002. Distribution and numbers of bowhead whales in the eastern Alaskan Beaufort Sea during late summer and autumn, 1979–2000. 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, Chapter 9. OCS Study MMS 2002-012; LGL Report TA2196-7. Report from LGL Limited, King City, Ontario for U.S. Minerals Management Service, Anchorage, Alaska and Herndon, Virginia. 37 p.

Moore, S.E. 2000. Variability of cetacean distribution and habitat selection in the Alaskan Arctic, autumn 1982–91. Arctic 53(4):448–460.

Moore, S.E., and DeMaster, D.P. 1998. Cetacean habitats in the Alaskan Arctic. Journal of Northwest Atlantic Fisheries Science 22:55–69.

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 No. 2. Lawrence, Kansas: The Society for Marine Mammalogy. 313–386.

Moore, S.E., Clarke, J.T., and Ljungblad, D.K. 1989. Bowhead whale (*Balaena mysticetus*) spatial and temporal distribution in the central Beaufort Sea during late summer and early fall 1979–86. Report of the International Whaling Commission 39:283–290.

Moore, S.E., George, J.C., Coyle, K.O., and Weingartner, T.J. 1995. Bowhead whales along the Chukotka coast in autumn. Arctic 48(2):155–160.

Moore, S.E., DeMaster, D.P., and Dayton, P.K. 2000. Cetacean habitat selection in the Alaskan Arctic during summer and autumn. Arctic 53(4):432–447.

Nerini, M.K., Braham, H.W., Marquette, W.M., and Rugh, D.J. 1984. Life history of the bowhead whale, *Balaena mysticetus* (Mammalia: Cetacea). Journal of Zoology, London 204(4): 443–468.

Richardson, W.J., ed. 1987. Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985-86. OCS Study MMS 87-0037. Report from LGL Ecological Research Associates Inc., Bryan, Texas, for U.S. Minerals Management Service, Reston, Virginia. 547 p. NTIS PB88-150271.

Richardson, W.J., and Thomson, D.H., eds. 2002. Bowhead whale feeding in the eastern Alaskan Beaufort Sea: Update of scientific and traditional information. OCS Study MMS 2002-012; LGL Report TA2196-7, 2 vols. Report from LGL Limited, King City, Ontario for U.S. Minerals Management Service, Anchorage, Alaska and Herndon, Virginia. http://www.mms.gov/alaska/reports/2002rpts/2002_012.pdf.

Richardson, W.J., Davis, R.A., Evans, C.R., Ljungblad, D.K., and Norton, P. 1987. Summer distribution of bowhead whales, *Balaena mysticetus*, relative to oil industry activities in the Canadian Beaufort Sea, 1980–84. Arctic 40(2):93–104.

Richardson, W.J., Greene, C.R., Jr., Hanna, J.S., Koski, W.R., Miller, G.W., Patenaude, N.J., and Smultea, M.A. 1995. Acoustic effects of oil production activities on bowhead and white whales visible during spring migration near Pt. Barrow, Alaska—1991 and 1994 phases. OCS Study MMS 95-0051; LGL Report TA954. Report from LGL Limited, King City, Ontario, for U.S. Minerals Management Service, Herndon, Virginia. 539 p. NTIS PB98-107667.

Rugh, D.J., Braham, H.W., and Miller, G.W. 1992. Methods for photographic identification of bowhead whales, *Balaena mysticetus*. Canadian Journal of Zoology 70(3):617–624.

Rugh, D.J., Zeh, J.E., Koski, W.R., Baraff, L.S., Miller, G.W., and Shelden, K.E.W. 1998. An improved system for scoring photo quality and whale identifiability in aerial photographs of bowhead whales. Report of the International Whaling Commission 48:501–512.

Thomas, T.A., Koski, W.R., Richardson, W.J., and Würsig, B. 2002. Surfacing, respiration and dive cycles of bowhead whales in the eastern Alaskan Beaufort Sea during late summer and autumn as related to age. 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, Chapter 14. OCS Study MMS 2002-012; LGL Report TA2196-7. Report from LGL Limited, King City, Ontario for U.S. Minerals Management Service, Anchorage, Alaska and Herndon, Virginia. 19 p.

Treacy, S.D. 1992. Aerial surveys of endangered whales in the Beaufort Sea, fall 1991. OCS Study MMS 92-0017. Anchorage, Alaska: U.S. Minerals Management Service. 93 p. NTIS PB93-193811.

———. 2000. Aerial surveys of endangered whales in the Beaufort Sea, fall 1998–1999. OCS Study MMS 2000-066. Anchorage, Alaska: U.S. Minerals Management Service. 135 p.

Treacy, S.D., Gleason, J.S., and Cowles, C.J. 2006. Offshore distances of bowhead whales (*Balaena mysticetus*) observed during fall in the Beaufort Sea, 1982–2000: An alternative interpretation. Arctic 59(1):83–90.

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, Chapter 12. OCS Study MMS 2002-012; LGL Report TA2196-7. Report from LGL Limited, King City, Ontario for U.S. Minerals Management Service, Anchorage, Alaska and Herndon, Virginia. 38 p.

Zeh, J., and Punt, A.E. 2005. Updated 1978–2001 abundance estimates and their correlations for the Bering-Chukchi-Beaufort seas stock of bowhead whales. Journal of Cetacean Research and Management 7(2):169–175.

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 No. 2. Lawrence, Kansas: The Society for Marine Mammalogy. 409–489.