Satellite-monitored movements of radio-tagged bowhead whales in the Beaufort and Chukchi seas during the late-summer feeding season and fall migration

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Abstract: From 30 August to 6 September 1992, we tagged 12 juvenile bowhead whales (*Balaena mysticetus*) with Argos satellite-monitored radio tags in the Canadian Beaufort Sea off the Mackenzie River Delta. Eight tags documented ≥9820 km of movements between 392 locations during 111 whale-tracking days. The whales did not move in unison. Individual movements and average speeds (1.1–5.8 km/h) varied widely. One whale stayed in Mackenzie Bay for 23.5 d, while the rest stayed an average of only 2.4 d. The majority of locations for all whales were in shallow water: 65% at <50 m depth and 87% at <100 m depth. Seven whales went into water >100 m deep and four were in water >500 m deep. The whale with the longest record traveled ≥3886 km to Siberia in 32.5 d, averaging 5.0 km/h. Its westerly route through the Beaufort and Chukchi seas was between 70° and 72°N and primarily in heavy ice (≥90% coverage), which was continuous west of 151°W. This whale's speed was faster, though not significantly, in heavy ice than in more open water. This is the first detailed documentation of the route and speed of a bowhead whale during its fall migration from Canadian to Russian waters.

Résumé : Entre le 30 août et le 6 septembre 1992, nous avons marqué chacune de 12 jeunes Baleines boréales (*Balaena mysticetus*) au moyen de marqueurs radio Argos suivis par satellite dans la mer de Beaufort au large du delta du Mackenzie. Huit marqueurs ont décrit ≥9820 km de déplacement entre 392 endroits au cours de 111 jours d'observation. Les baleines ne se déplaçaient pas à l'unisson. Les déplacements et les vitesses moyennes de nage variaient considérablement (1,1 à 5,8 km/h). Une baleine est restée dans la baie de Mackenzie pendant 23,5 jours alors que les autres baleines n'y ont fait qu'un séjour de 2,4 jours en moyenne. La plupart des endroits fréquentés par les baleines étaient en eau peu profonde, 65 % à moins de 50 m et 87 % à moins de 100 m. Sept baleines ont gagné les eaux de plus de 100 m de profondeur et quatre ont été trouvées dans des eaux de plus de 500 m de profondeur. La baleine qui a battu tous les records a parcouru ≥3886 km jusqu'en Sibérie en 32,5 jours, à raison de 5,0 km/h en moyenne. Son trajet vers l'ouest à travers la mer de Beaufort et la mer de Choukotchee était entre 70° et 72°N, surtout dans de la glace épaisse (couvrant ≥90 % de la surface) qui était continue jusqu'à l'ouest de 151°O. Sa vitesse de nage était plus rapide dans les glaces que dans l'eau libre, quoique non significativement. Il s'agit là d'une description inédite de l'itinéraire détaillé et de la vitesse précise d'une Baleine boréale durant sa migration d'automne des eaux canadiennes aux eaux russes.

[Traduit par la Rédaction]

Introduction

Despite at least 2000 years of subsistence hunting by indigenous people (Stoker and Krupnik 1993), the Bering Sea stock of the bowhead whale (*Balaena mysticetus*) did not become endangered (Klinowska 1991) until it was hunted commercially (Bockstoce 1986; Bockstoce and Burns 1993). Between 1848 and 1914, whalers killed over 20 000 bowhead whales (Bockstoce and Botkin 1983), reducing the Bering Sea population to approximately 3000 (Woodby and Botkin 1983). Based on visual and acoustic surveys (Clark and Ellison 1988, 1989), the population is presently estimated at 7500 (Zeh et al. 1993) and is growing at about 3% per year (Zeh et al. 1991) despite an annual subsistence harvest of <1%.

What is known of the generalized seasonal movements of bowhead whales belonging to the Bering Sea stock has been described by Moore and Reeves (1993). Subsistence-hunting

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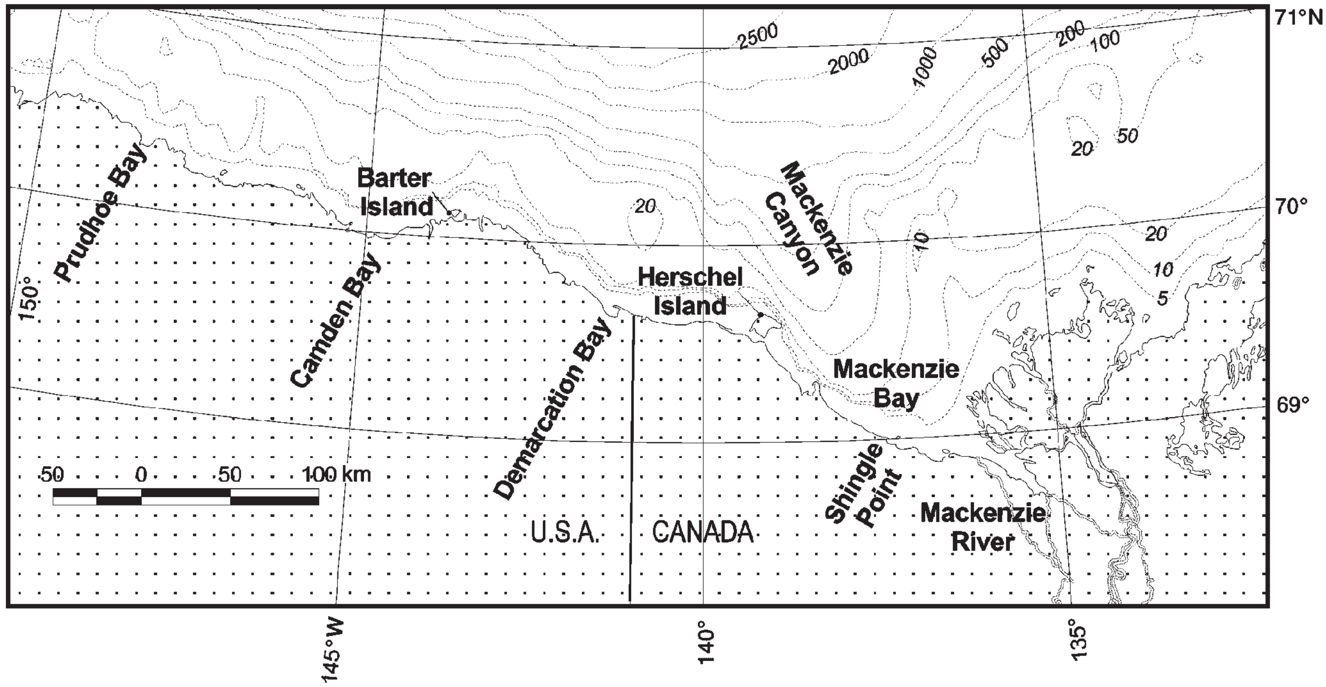
Fig. 1. The study area, showing the area of tagging of bowhead whales (*Balaena mysticetus*) and places mentioned throughout the text.



and commercial-whaling records provide much of what we know about bowhead whales in the western hemisphere. The whales winter south of the Bering Strait, owing to heavy ice farther north. In the spring, they migrate north into the Chukchi Sea along the northwest coast of Alaska and then east into the Beaufort Sea, where they feed during the summer (Lowry 1993). The spring migration has been studied intensively in order to estimate the population (Zeh et al. 1993). In the fall, the whales migrate west out of the Beaufort Sea to the Chukchi Sea and eventually south to the Bering Sea.

The summer feeding season and fall migration have been the focus of considerable research during the last 15 years, owing to the potential for disturbance by offshore petroleum development. The short open-water season, the large areas that bowhead whales occupy, and other logistic constraints have limited the amount and types of data collected by observers. Researchers have primarily used aircraft as observation platforms for watching bowhead whales feed (Würsig et al. 1985; Ljungblad et al. 1986), determining their distribution, and monitoring their westward migration (Ljungblad et al. 1988; Treacy 1998[3]).

Understanding the variability in habitat utilization by bowhead whales in this population requires detailed information about the movements of individual animals. Examining the movements of individual bowhead whales has been limited to a few photographic identification and conventional telemetry studies (Davis et al. 1983[4]; Richardson et al. 1987; Wartzok et al. 1989[5], 1990[6]). In this study, satellite-monitored radio tags were used to determine the timing, route, and movement rates of individual whales during the late summer and fall.

Methods

We used the Argos data collection and location system (ADCLS) to track radio-tagged whales. Argos receivers are on board the National Oceanic and Atmospheric Administration television infrared observation satellites (TIROS-N) in sun-synchronous polar orbits (Harris et al. 1990). This system locates transmitters by means of Doppler shift resulting from movements of the satellite.

We encountered only juvenile–subadult whales (≤13 m long) (Koski et al. 1993). We tagged 12 bowhead whales of unknown sex between 30 August and 6 September 1992. Whales were tagged within a 40-km^2 area near Shingle Point, Northwest Territories, Canada (68°59′N, 137°26′W; Fig. 1). The estimated lengths of tagged whales ranged from 8 to 12 m.

We deployed tags from a 2.5 m long platform extending 45° off the starboard bow of the 13.7-m twin-diesel R/V *Annika Marie*. Deployment, attachment, and tag design were similar to those used for North Atlantic right whales, *Eubalaena glacialis* (Mate et al. 1997). Each tag was applied as a projectile from a compound crossbow, approximately 3 m behind the blowhole, near the middorsal line. Whales were tagged at distances of 3–8 m in water

[3] S. Treacy 1998. Aerial surveys of endangered whales in the Beaufort Sea, fall 1997. U.S. Minerals Management Service, Alaska Outer Continental Shelf Region.

[4] R.A. Davis, W.R. Koski, and G.W. Miller 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. Final report by LGL Ltd., Toronto, to the National Marine Mammal Laboratory.

[5] D. Wartzok, W.A. Watkins, B. Würsig, and C.I. Malme, 1989. Movements and behaviors of bowhead whales in response to repeated exposures to noises associated with industrial activities in the Beaufort Sea. Report to Amoco Production Co., P.O. Box 800, Denver, CO 80201, U.S.A.

[6] D. Wartzok, W.A. Watkins, B. Würsig, J. Guerrero, and J. Schoenherr, 1990. Movements and behavior of bowhead whales. Report from Purdue University, Fort Wayne, Ind., for Amoco Production Co., P.O. Box 800, Denver, CO 80201, U.S.A.

Table 1. Length, tagging location, qualitative judgment regarding tag position, and characteristics of transmitter performance for bowhead whales equipped with Argos radio tags between 30 August and 6 September 1992.

		Tagging location			Transmitter performance			
Tag No.	Approximate length of whale (m)	Latitude N	Longitude W	Tag position	Total no. of transmissions	No. of days to last transmission	Last status message[a]	Voltage (V)
DZ-1	10	69°01′	37°21′	Excellent	984	32.5	31.0	7.23[b]
DZ-2	10–11	69°06′	37°25′	Good	140	8.1	5.8	8.51[b]
DZ-3	8	69°06′	37°05′	Excellent	66	3.1	1.3	9.79
DZ-4	10	69°07′	37°06′	Excellent	304	10.9	8.8	8.06[b]
DZ-5	10	69°07′	37°02′	Excellent	202	9.0	8.2	8.70[b]
DZ-6	8–9	69°07′	37°06′	Good	211	10.1	10.1	6.59[b]
DZ-7	11–12	69°01′	37°20′	Poor	3	25.7	None	—
DZ-8	9	69°02′	37°19′	Good	9	3.2	None	—
DZ-9	8–9	69 06′	37°04′	Poor	5	48.3	None	—
DZ-10	8–9	69°06′	37°10′	Poor	3	8.5	None	—
D-1	8	69°03′	37°14′	Good	60	23.5	na	na
D-2	8.5–9.5	69°05′	37°10′	Excellent	73	16.5	na	na

[a]Days after tagging.
[b]Battery voltage probably limited the useful life of the tag.

≤10 m deep. Whales were approached from the rear as they began a surfacing sequence of respirations after a long dive. We found it advantageous to approach animals in shallow water, where we could monitor their underwater progress by observing surface eddies from their flukes or their bow wake.

Two types of tags were deployed: two "duration" tags (D-1 and D-2) and 10 "duration–depth" tags (DZ-1 to DZ-10). Tags were composed of a 400-mW Telonics ST-6 asynchronous ultra high frequency (UHF) radio transmitter, a controller board supplied by Telonics, Inc. or Wildlife Computers Inc., and eight Duracell® 2/3-A lithium – manganese dioxide batteries supplying 12 V. Components were packaged in stainless-steel cylinders 189 mm long and 49 mm in diameter (D tags) or 192 mm long and 54 mm in diameter (DZ tags). An entire tag assembly weighed 0.46 (D tags) or 0.80 (DZ tags) kg in air. Each tag collected dive and surfacing information, which is reported in the companion paper (Krutzikowsky and Mate 2000); this paper reports only the movements of the tagged whales.

D tags transmitted at surfacings during the first 100 consecutive minutes of every 12 h. DZ tags transmitted at surfacings throughout the day. Times and dates are reported in universal coordinated time (UTC). Both types of tag were programmed to ensure that transmissions occurred no more frequently than once every 40 s. Once every 15 transmissions, DZ tags transmitted a utility message that included battery voltage. Radiated power varied with voltage and was estimated to be 400 mW at 12.0 V, but only 250 mW at 9.5 V (S.M. Tomkiewicz, personal communication). Based on battery capacity and energy requirements, we estimated the number of transmissions to predict a functional life of 1 month for DZ tags and 6 months for D tags.

Two satellites each provided 12–14 passes/d over the study area. D tags could utilize a maximum of four of these passes because of their transmission schedule. Satellites were within range for up to 17 min (average duration 10 min). Argos defines four location classes based on the number of messages received and their spacing during a satellite pass (Argos 1990). Argos predicts that 67% of their locations for classes LC1, LC2, and LC3 will be within 1000, 350, and 150 m of their true location, respectively. LC0 locations do not have an estimated accuracy. Locations were eliminated from analysis when (*i*) they were conspicuously on land (>5 km inland, allowing for ambiguity in Argos locations near shore) or (*ii*) they resulted in speeds >25 km/h between adjacent locations. We observed bowhead whales swimming at approximately 20 km/h for short periods and picked a value 25% higher (25 km/h) as our screening criterion for "allowable" swimming speeds. The speed criterion helped screen for some of the locational errors associated with all Argos locations (Stewert et al. 1989; Harris et al. 1990; Keating et al. 1991; Mate et al. 1997). Eliminating locations using the two screening criteria was an iterative process. Dive depths recorded by DZ tags (Krutzikowsky and Mate 2000) were considered in choosing between alternative locations in different water depths that conformed to the screening criteria. Only locations that met our screening criteria were plotted on maps or used for subsequent calculations.

Geographic figures were created using shoreline data, Arc/INFO®, and ArcView® software (Environmental Systems Research Institute, Inc., Redlands, Calif.) on an IBM-based PC. Shallow bathymetry (≤200 m) was digitized from NOAA chart No. 16003, and the remaining bathymetry was derived from gridded ETOPO-5 data (National Geophysical Data Center, ETOPO-5 Bathymetry/Topography Data) and smoothed and contoured with Arc/INFO®. Ice cover at whale locations was evaluated from daily ice-analysis charts issued by Environment Canada's Ice Centre in Ottawa and (or) satellite images collected at the Anchorage branch of the U.S. National Weather Service.

Speeds were calculated using the computed distances and times between locations. "Overall speed" refers to the total distance divided by the total time tracked. In a few cases, a track was separated into sections and the speeds describing these track sections are calculated as "distance in track section divided by time in track section."

Results

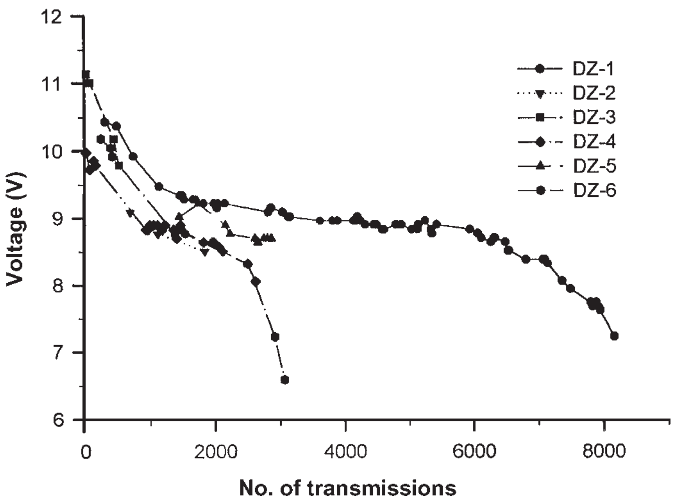
Tag operation

Transmissions were received from all 12 tags (Table 1) up to a maximum of 48.3 d (mean = 16.6 d, SD = 13.55 d, n = 12). Only eight tags had enough transmissions during individual orbits to provide useful locations (Table 2). Locations were acquired only from tags with good or excellent middorsal placement. The D tags, with a conservative 14% duty cycle (200 min of transmission/d), provided locations for an average of 20.0 d (SD = 4.95 d, n = 2) compared with

Table 2. Total distances traveled, overall average speeds, durations of tag operation, and location data (number received, number retained after editing, and category) for bowhead whales equipped with Argos radio tags applied between 30 August and 6 September 1992.

Tag No.	Total distance traveled (km)	Overall avg. speed (km/h)	No. of days to last location	No. of locations received	No. of locations retained	Location category LC0	LC1	LC2	LC3
DZ-1	3886	5.0	32.5	277	206	181	18	5	2
DZ-2	804	4.2	7.9	38	19	19	0	0	0
DZ-3	206	3.5	2.5	17	5	3	2	0	0
DZ-4	1080	4.1	10.9	80	64	56	8	0	0
DZ-5	781	3.9	8.2	42	34	24	4	6	0
DZ-6	1391	5.8	10.1	64	39	33	3	3	0
D-1	619	1.1	23.5	15	9	9	0	0	0
D-2	1053	2.8	15.5	20	16	16	0	0	0
Total	9820		111.1	553	392	341	35	14	2
Mean	1227.5	3.80	13.89	69.1	49.0	42.6	4.4	1.7	0.2

Fig. 2. Voltages of Argos radio tags over the course of this study plotted against the total number of transmissions.



the 15.9 d (SD = 14.79 d, n = 10) for the DZ tags, which could transmit at any time of day. Three tags that were poorly positioned (so far from the midline that they rarely surfaced) seldom transmitted (Table 1). We received few transmissions from these three tags (mean = 3.7, SD = 1.15, n = 3) but heard from them for longer periods (mean = 27.5 d, SD = 19.96 d, n = 3) than from the other tags (mean = 13.0 d, SD = 9.68 d, n = 9). Status messages measuring battery voltage revealed substantial differences between tags. Of six tags with utility-status messages, five reported a battery voltage below 9 V within 5–11 d (Fig. 2, Table 1). Tag DZ-6 had a lower voltage after 10.1 d of operation than tag DZ-1 had after 31.0 d.

Locations and movements

Argos calculated 553 locations for eight whales, but 161 (29%) did not meet our screening criteria and were eliminated (Table 2). The percentage of unsuitable locations varied from 26 to 71% among whales. The remaining 392 screened locations plus the tagging locations accounted for 111.1 d of tracking and a distance of at least 9820 km between consecutive locations (Table 2). Individual whales were located between 5 and 206 times over 2.5–32.5 d and traveled between 206 and 3886 km. The number of usable daily locations varied among whales, from 0.4 to 6.3. The overall speed for individual whales varied from 1.1 to 5.8 km/h (mean = 3.80 km/h, SD = 1.418 km/h; Table 2).

Table 3. Water depths for tagged bowhead whales at the tagging site and subsequent satellite-acquired locations.

Tag No.	Water depth (m) 0–50	51–100	101–200	201–500	>500	Total
DZ-1	131	62	6	5	3	207
DZ-2	18	0	1	1	0	20
DZ-3	5	0	1	0	0	6
DZ-4	32	22	11	0	0	65
DZ-5	18	2	2	1	12	35
DZ-6	30	3	1	1	5	40
D-1	10	0	0	0	0	10
D-2	15	0	1	0	1	17
Total	259	89	23	8	21	400

The movements and habitat characteristics of the tagged whales were diverse. Seven of the eight animals moved out of Mackenzie Bay during monitoring. Six animals moved west and (or) north of Herschel Island. The majority of locations from all whales were in shallow water, with 65% in water <50 m deep and 87% in water <100 m deep (Table 3). However, most whales did venture into deeper water. Of eight tagged whales with locations, seven were located in water >100 m deep and four were in water >500 m deep.

Movements of individuals

This section briefly summarizes the movements of tagged whales from the least complicated to the most extensive. Whale DZ-3 was tracked for only 2.5 d between five locations (206 km) clustered within 85 km of the tagging site (Fig. 3), resulting in 2.0 locations/d and an overall speed of 3.5 km/h. All locations were in ice-free water <200 m deep. Whale D-1 limited its activities to the Mackenzie Bay region, traveling at least 619 km during 23.5 d between the

Fig. 3. Track of whale DZ-3 in Mackenzie Bay obtained using satellite telemetry; ★, tag-deployment location. Numbers are days elapsed since tag deployment on 5 September 1992 at 19:29 UTC. Depth contours are in metres.

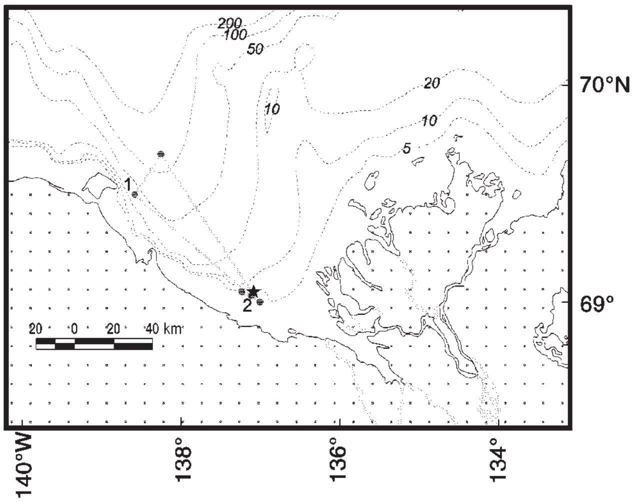


Fig. 4. Track of whale D-1 in Mackenzie Bay obtained using satellite telemetry; ★, tag-deployment location. Numbers are days elapsed since tag deployment on 6 September 1992 at 03:49 UTC. Depth contours are in metres.

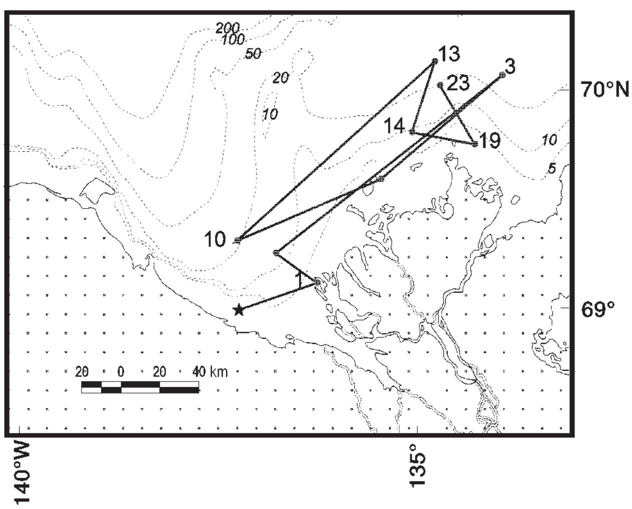


Fig. 5. Track of bowhead whale DZ-4 in the region around Mackenzie Bay obtained using satellite telemetry; ★, tag-deployment location. Numbers are days elapsed since tag deployment on 3 September 1992 at 20:49 UTC. Depth contours are in metres.

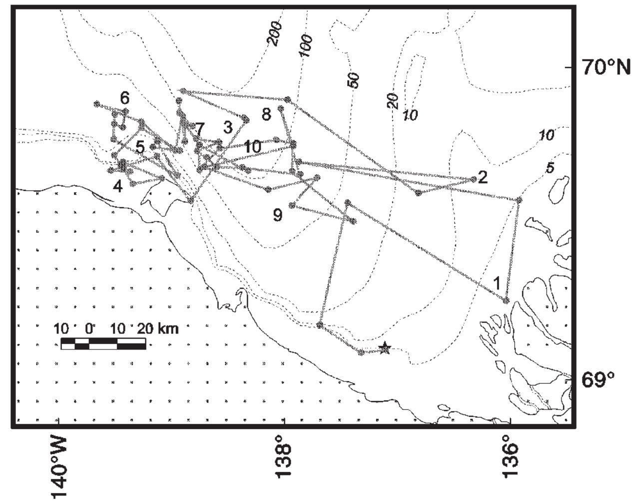
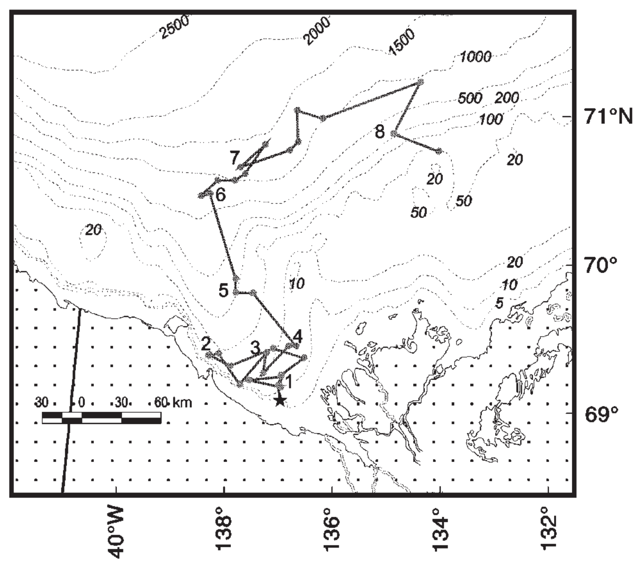


Fig. 6. Track of bowhead whale DZ-5 in the region around Mackenzie Bay obtained using satellite telemetry; ★, tag-deployment location. Numbers are days elapsed since tag deployment on 3 September 1992 at 21:29 UTC. Depth contours are in metres.



tagging site and nine locations (0.4 locations/d). All locations were within 185 km of the tagging site near the Mackenzie River Delta in water <25 m deep (Fig. 4). Whale D-1 had the slowest overall speed (1.1 km/h) of all whales tracked (Table 2). The last two locations, received in late September, were 4 d apart in an area with ≥80% ice cover, by which time the migration route to the west was ≥90% ice-covered.

Two whales (DZ-4 and DZ-5) spent their monitored time in just three areas. In 10.9 d, whale DZ-4 traveled 1080 km between 64 satellite-acquired locations. This resulted in 5.9 locations/d and an overall speed of 4.1 km/h during travel between Mackenzie Bay, Herschel Island, and Mackenzie Canyon (Fig. 5). The whale's locations were in water 5–200 m deep. After spending several days west of Herschel Island in water <60 m deep, this animal moved east of the island into waters 50–200 m deep in Mackenzie Canyon, with a short excursion back into Mackenzie Bay. All locations were in ice-free water.

In 8.2 d, whale DZ-5 moved 781 km (overall speed 3.9 km/h) between the tagging site and 34 satellite-acquired locations (4.1 locations/d; Fig. 6). During the first 4 d, this whale traveled in an area within 60 km of the tagging site in water <50 m deep, then north along the eastern side of Mackenzie Canyon to waters 1000–1500 m deep. The second half of its track was characterized by deeper water. This whale was located in deep water more frequently than any other whale (34% of its locations were in water >500 m

Fig. 7. Track of bowhead whale DZ-2 from Mackenzie Bay west to Demarcation Bay, then north and east to Mackenzie Canyon, obtained using satellite telemetry; ★, tag-deployment location. Numbers are days elapsed since tag deployment on 2 September 1992 at 23:30 UTC. Depth contours are in metres.

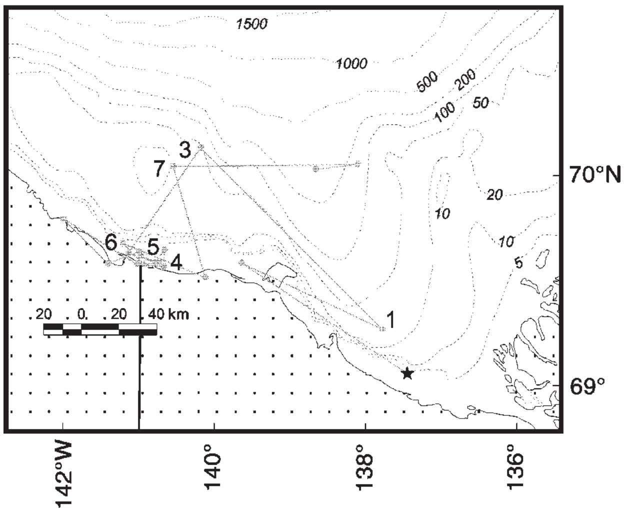
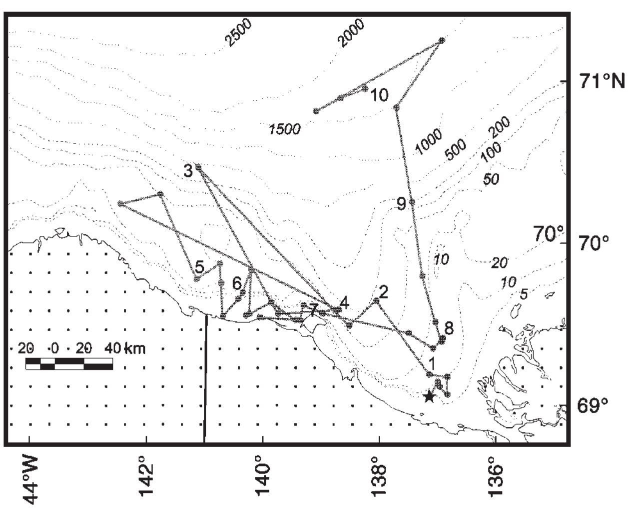


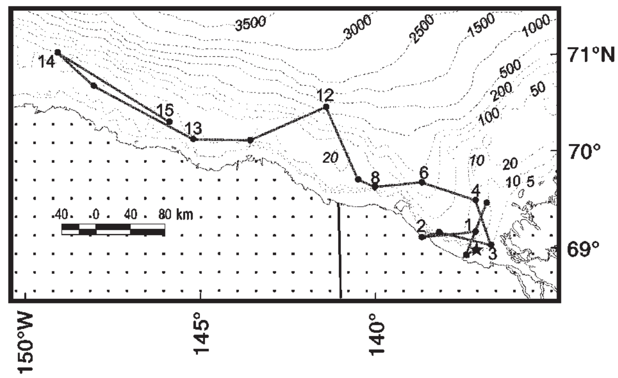
Fig. 8. Track of bowhead whale DZ-6 in the region between Mackenzie Bay and Barter Island obtained using satellite telemetry; ★, tag-deployment location. Numbers are days elapsed since tag deployment on 4 September 1992 at 18:06 UTC. Depth contours are in metres.



deep) and had locations in all depth categories (Table 3). Ice cover was 10–50% at six of its last nine locations.

Whales DZ-2 and DZ-6 spent part of their time traveling west, DZ-2 as far as Demarcation Bay (Fig. 7) and DZ-6 to within 43 km of Barter Island (Fig. 8), before again heading east. DZ-2 traveled 804 km (overall speed 4.2 km/h) between the tagging site and 19 satellite-acquired locations (2.4 locations/d) in 7.9 d (Fig. 7). In this short period, the animal went to Herschel Island, returned to Mackenzie Bay, went northwest nearly to the shelf break off Demarcation Bay, inshore to Demarcation Bay for 3 d, and then back offshore and east to Mackenzie Canyon into water >300 m

Fig. 9. Track of bowhead whale D-2 in the region from Mackenzie Bay westward past Camden Bay obtained using satellite telemetry; ★, tag-deployment location. Numbers are days elapsed since tag deployment on 6 September 1992 at 3:20 UTC. Depth contours are in metres.



deep. Prior to the period spent in Mackenzie Canyon, all locations were in water <50 m deep.

Whale DZ-6 had the fastest overall speed (5.8 km/h) and second-longest track among all whales (Table 2), moving 1391 km from the tagging site to 39 satellite-acquired locations (3.9 locations/d) in 10.1 d (Fig. 8). This whale visited and returned to several diverse habitats. The first 2 d after tagging were spent in Mackenzie Bay, followed by a 1-d visit to the east and west sides of Herschel Island, and then into deep water offshore from Demarcation Bay. Over the next 6 d, this animal returned to both the west and east sides of Herschel Island, traveled west almost to Barter Island (continuing offshore and returning to Demarcation Bay), and then traveled past Herschel Island and back to Mackenzie Bay. Finally, the animal traveled north into deep-basin water (>1500 m), where it encountered up to 70% ice cover. This animal had locations in all water-depth categories (Table 3): 74% were in water <50 m deep, 13% in water 50–500 m deep, and 13% in water >500 m deep. Locations off Demarcation Bay included water <20 m deep nearshore, >50 m deep 50 km offshore, and ~500 m deep 100 km offshore.

The two whales with the most westerly tracks, D-2 and DZ-1, were equipped with different types of tags. The different rates at which locations were acquired (1.0 and 6.3 locations/d for D-2 and DZ-1, respectively) reflects in part the ratio of their daily transmission schedules (3.3 vs. 24 h/d). Whale D-2 traveled 1053 km (Fig. 9) between the tagging site and 16 satellite-acquired locations (1/d) in 15.5 d (overall speed 2.8 km/h). Whale D-2 spent the first 4 d in Mackenzie Bay. By day 6 it was in Mackenzie Canyon. Eight days after tagging, it was between Herschel Island and Demarcation Bay. Four days later it headed north offshore to water >500 m deep. During the last 4 d of tracking, this whale moved inshore to water 20–50 m deep, west across Camden Bay, and northwest past Prudhoe Bay to 150°W, before reversing course for 153 km, almost to Camden Bay. Canadian Ice Analysis charts for 19 September, 13 d after tagging, indicate ice-free water at the first location of the day. However, the Kuvlum exploratory offshore drilling site (70.3159°N, 145.4197°W), just 2.3 km away, was not active, owing to heavy ice (Brewer et al. 1993[7]). Ice cover at locations during the last 7 d varied from 0 to 90%. The most westerly location, at 150°W, was 90% ice-covered.

Whale DZ-1 was tracked farther (3886 km) and for a longer period (32.5 d) than any other whale (Fig. 10). With an overall speed of 5.0 km/h, DZ-1 was the second fastest of all tagged whales. The 206 satellite-acquired locations (6.3 locations/d) represented all water-depth categories (Table 3).

The first half (16 d) of the track of whale DZ-1 meandered as it moved 12° west, from 135°38′W to 147°36′W, sometimes backtracking east (Fig. 10). During the last 16 d, it moved consistently westward 30° from 147°W to 177°W. The overall speeds for the two segments were similar (4.8 and 5.1 km/h). Starting nearshore, whale DZ-1 moved northeast in the shallow water (<20 m deep) of Mackenzie Bay, northwest to the western side of Mackenzie Canyon, to Herschel Island's northeast shoreline, west to an area 35 km north of Demarcation Bay, northeast to the Arctic Basin (1000 m deep), west to the shelf break 80–100 km north of Demarcation Bay, northeast to the basin again, south to Herschel Island, west-northwest to Demarcation Bay (25 km offshore), nearshore until rounding Point Martin 50 km from shore, back to nearshore along the 20-m contour from northwest of Barter Island through the eastern half of Camden Bay, and northwest to the shelf break about 75 km off Prudhoe Bay.

During the remaining time, whale DZ-1 moved west to very shallow water at Cape Halkett, northwest to 10 km off Point Barrow, generally west across the Chukchi Sea (roughly between latitudes 71° and 72°N), and then west-southwest to a location south of Wrangell Island within 175 km of the Chukchi Peninsula. This is the first detailed record of the route and speed of migration for a bowhead whale from Canada to Russia, and the only record of an individual whale's movements through the Chukchi Sea.

This animal first encountered ice cover (30%) at its most northern Mackenzie Canyon location on 11 September, 8 d after tagging. As it moved west from 151°W on 20 September until the end of its track on 5 October, this whale was in ice cover >90%. Twenty-five locations were classed as >LC0; five of these (20%) occurred during an 8-h period on the day before the whale encountered >90% ice cover. Satellite images of the ice in the Chukchi Sea revealed that the track of whale DZ-1 was along the edge of heavy ice (G. Hufford, personal communication), where four of the six locations >LC0 in the Chukchi Sea occurred.

Site preference

It is difficult to evaluate site preferences when the sample size is so small, the study period is short, and the study is carried out at the transition between feeding and migrating seasons. Nonetheless, some site preferences are suggested by the amount of time whales spent in certain areas, the number of whales visiting these areas, and the number of times individual whales revisited specific areas. Obviously, all tagged whales were in Mackenzie Bay at the start of our study. One whale stayed in Mackenzie Bay for 23.5 d, the duration of its transmitter's operation. All other whales left the bay, on average, 2.4 d (SD = 1.79 d, n = 7) after tagging. From 1 to 8 d after leaving Mackenzie Bay (mean = 3.1 d, SD = 2.78 d, n = 4), four whales each returned to the Bay for a single day. Six whales visited Mackenzie Canyon (mean = 1.0 d, SD = 0.62 d, n = 8 visits), five were located at Herschel Island (mean = 1.1 d, SD = 1.07 d, n = 8 visits), and four used the nearshore (mean = 1.5 d, SD = 1.02 d, n = 5 visits) and offshore (mean = 1.8 d, SD = 1.40 d, n = 6 visits) waters off Demarcation Bay.

Discussion

As all the whales we tagged were juveniles, generalizing these data in order to characterize the entire population is inappropriate. Throughout this discussion, we acknowledge what little is known of age, sex, and reproductive-class differences in migratory timing and habitat preferences.

Unfortunately, the substantial differences seen in bowhead whale distribution from year to year suggest that much of the variability may be due to oceanographic factors affecting prey distribution.

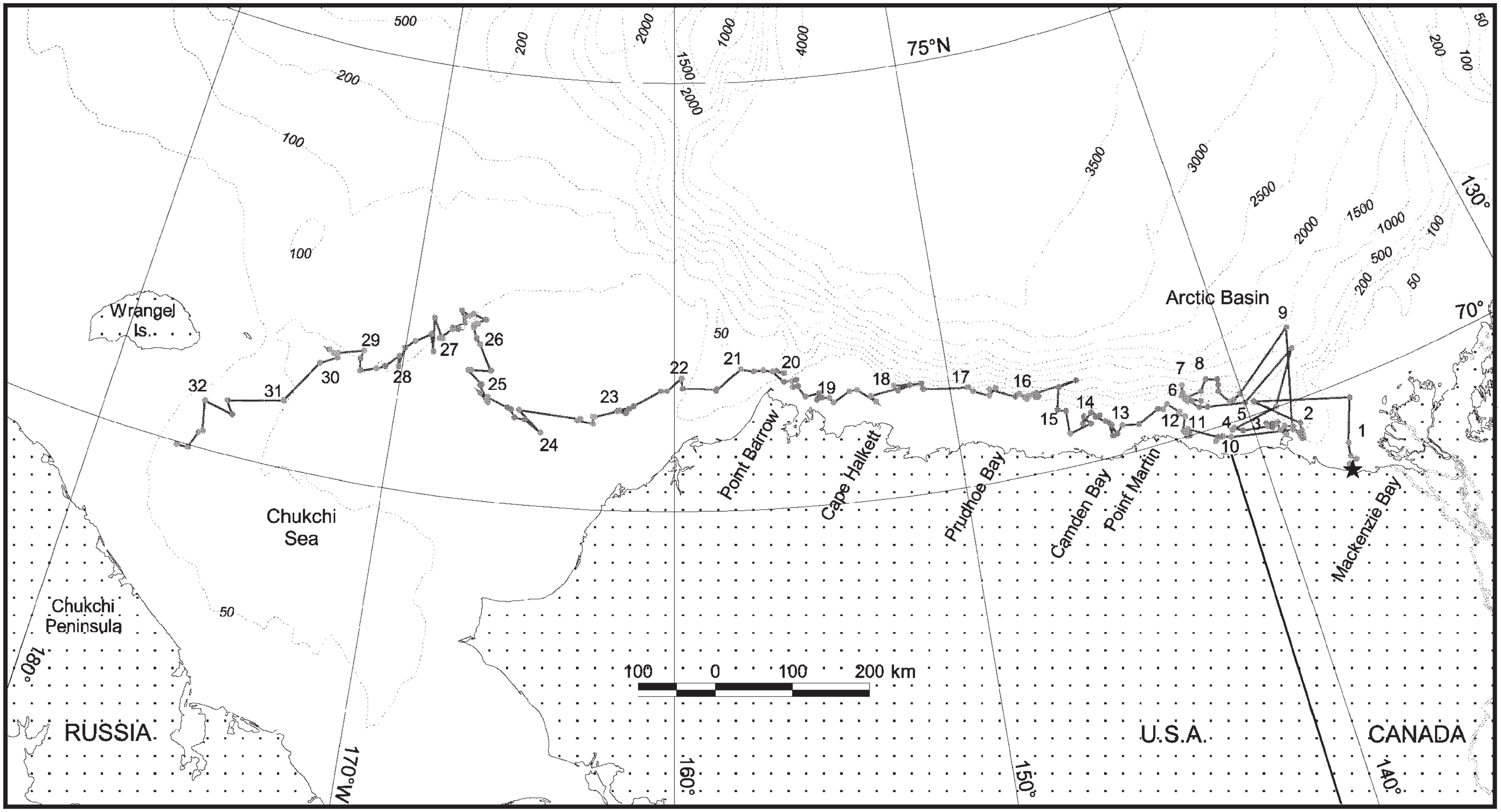
Caution must be exercised in interpreting the "whale tracks" shown here. The lines connecting sequential locations merely provide chronological guidance and do not necessarily represent the route of travel. Nonetheless, the shortest distance (straight line) between locations is used as the minimum distance traveled and as a basis for speed calculations. The actual distances whales traveled and their speeds may be different. Because Argos locations were not determined routinely at regular time intervals, the distances between points do not reflect differences in travel speed. Further, because of our editing criteria and ambiguities in Argos locations, the amounts of error between adjacent locations can vary. Consequently, a detailed assessment of individual segment speeds could be misleading.

Transmitter performance

Tag longevity and performance on bowhead whales were likely affected by tag placement, transmission schedule, battery voltage, and possibly ice conditions. Tag attachment on bowhead whales was documented by receiving transmissions up to 48.3 d after tagging (Table 1), 15% better than the record for the same tag type used on North Atlantic right whales (Mate et al. 1997). Low-lateral (poor) rather than middorsal (good and excellent) tag placement resulted in fewer transmissions and no locations for tags DZ-7, DZ-9, and DZ-10 because the tags did not come out of the water frequently. The less dorsal attachment position probably made these tags less vulnerable to being scraped by ice. Also, since the tags did not transmit as frequently, battery power was conserved, resulting in a potentially longer average transmitter life. Improvements in tag design that should enhance attachment longevity include smaller tags; implanting most of the tag to reduce hydrodynamic drag; a greater surface area for subdermal attachments, to reduce tag move-

[7] K.D. Brewer, M.L. Gallagher, P.R. Regos, P.E. Isert, and J.D. Hall. 1993. Kuvlum #1 exploration prospect, site specific monitoring program. Final report by ARCO Alaska, Inc.

Fig. 10. Track of bowhead whale DZ-1 from Mackenzie Bay through the Chukchi Sea obtained using satellite telemetry; ★, tag-deployment location. Numbers are days elapsed since tag deployment on 2 September 1992 at 20:51 UTC. Depth contours are in metres.



ment; and constructing tags out of materials that promote tissue adhesion.

When this study was conducted, Service Argos limited transmissions to no more than one every 40 s to avoid overloading the satellite receivers. Argos presently allows a 10-s repetition rate for tags deployed on whales, to obtain more and better quality locations (Mate et al. 1998). Their regular and short-duration surfacings of whales reduce the risk of overloading the Argos receiver systems. This change has resulted in more messages being received per orbit, a higher percentage of orbits having locations, and locations being of higher quality (more accurate) (Mate et al. 1998).

Low temperatures and high transmission rates likely contributed to the short battery life of many of the DZ transmitters. It is common for the ampere-hour capacity of lithium (and most other types of) batteries to drop by 50% at temperatures near freezing. Battery voltage monitored on bowhead whale DZ transmitters dropped to <9 V within only 8–11 d, and may have contributed to the short operational life of some tags. The appropriate management of battery power is essential in designing a satellite-monitored radio-tag experiment in order to achieve experimental goals. The two extreme strategies are (1) tracking for a shorter period by transmitting during all satellite opportunities, in order to get fine detail (lots of locations), or (2) tracking for a longer time period with fewer transmissions (and hence locations) per day, to maximize range information such as migrations. We saw differences in tag longevity that coincided with the total number of transmissions: two poorly placed DZ tags, which rarely transmitted, lasted, on average, 27.5 d; two low duty cycle D tags (transmitting 14% of available time) lasted, on average, 20 d; and seven DZ tags that were well placed and transmitted at every opportunity lasted 15.9 d. However, our sample sizes were small and we know that other factors besides transmission strategy may have affected transmitter life (i.e., position and attachment). A compromise strategy would be to sample intensively for a modest period (several orbits) once every few days or weeks. To further conserve power, we can now program tags to transmit just during selected predictable satellite orbits. Because TIROS satellites are in sun-synchronous orbits, their coverage of a specific longitude occurs during the same solar time periods each day, at sunrise, for example. Thus, the appropriate time to transmit to a satellite is more difficult to predict if the extent or timing of east–west movements is not well known. If east–west directional movements are expected but not known, longer duty cycles may be necessary to detect such movements. This is less of a factor at high latitudes. Transmitters above 75° are receivable during all satellite orbits.

If transmitters become small enough in the future to be almost entirely implanted, the higher subdermal temperatures may allow for more efficient battery operation and result in higher radiated power and a greater number of received transmissions. We examined a number of strategies for regenerating power in order to extend battery life. Because multiple transmissions are required in a single orbit to obtain a location, slow (trickle) charging techniques (usually requiring bulky capacitors) are not practical. Further, rechargeable batteries typically take up considerably more space for the same ampere-hour capacity than the lithium cells we chose. Whales do not spend enough time at the surface for solar recharging, even in tropical latitudes and bowhead whales are at an added disadvantage because of the short day lengths of late fall and winter. Unfortunately, propellor-driven generators will increase drag and vibration, but more passive charging systems using pressure or temperature may prove effective. The amount of power needed probably precludes sacrificial metal (galvanic action) systems that might also be an irritant to the whale's tissues. Once improved attachments extend the time that tags stay on whales, it may be worth exploring recharging systems further.

Migratory timing and dispersal

Although all eight subadult whales were tagged at one site during a single week, they did not subsequently move in unison. Thus, the westward migration does not appear to start in response to a single environmental cue. Instead, whales moved in many directions and into waters of different depths. For example, on 29 September, whale D-1 was still in Mackenzie Bay, 154 km northeast of its tagging site (Fig. 4), while whale DZ-1 was crossing the Chukchi Sea, 1152 km west of where it was tagged (Fig. 10). Barter Island whalers have said that juveniles migrate before adults (Braham et al. 1984), but the difference between whales D-1 and DZ-1 (the larger of the two juvenile whales; Table 1) demonstrates the variability among individuals.

The Minerals Management Service (U.S. Department of the Interior) has used counts of westward migrating whales to estimate when half the population has passed specific areas, in order to regulate offshore oil- and gas-drilling activities (Treacy 1998, see footnote 3). In future attempts to estimate the bowhead whale population from counts of migrating individuals, the finding that some bowhead whales reverse their direction once they start west will need to be taken into consideration. The eastward reversal by whale D-2 after it passed Prudhoe Bay in late September indicates that some whales meander and reverse course even after making substantial westward progress. After crossing into Alaskan waters, three other whales (DZ-1, DZ-2, and DZ-6) backtracked to Canadian waters and then moved west again into Alaskan waters at least once.

Migration route

The route of whale DZ-1 in the U.S. Beaufort Sea was quite similar to the highest density of bowhead whale sightings from pooled (1979–1989) aerial-survey data (Moore and Reeves 1993). Our study, like those of Wartzok et al. (1989, see footnote 5, 1990, see footnote 6), shows that animals do not always take direct routes and do pause from time to time. Variations in the migration routes and rates of movement may be due to different age and (or) sex classes and annual differences in prey, summer feeding success, and (or) ice conditions.

Moore and Clarke (1990) speculated that in the Chukchi Sea, there were two routes bowhead whales might travel west of Point Barrow. One route, to the southwest, was based on aerial-survey sightings. The second, a more northerly route along latitude 72°N, was created without a statistical basis. This line fits the track of whale DZ-1 reasonably well. It is presently impossible to estimate what proportion of the population may travel each of these routes, as oppor-

Table 4. Speeds of individual radio-tagged bowhead whales derived from conventional (VHF and HF) and satellite-monitored telemetry.

Year	n	Distance (km)	Duration (d)	Speed (km/d)	Source
1986	2	46–76	2–4	19–23	Richardson et al. 1987
1988	2	915–1291	13–17	70–76[a]	Wartzok et al. 1989, see footnote 5
1989	4	554–1347	18–36	36–60	Wartzok et al. 1990, see footnote 6
1992	8	206–3886	2–33	26–139	This study
Mean		1228	14	88	

[a]One whale averaged 98 km/d over a 6-d period.

tunities to "observe" both routes are not equal. Nonetheless, whalers have given accounts of hunting bowhead whales near Herald Shoal (Fig. 10) during September–October (Bockstoce and Botkin 1983), which is the time of year that whale DZ-1 crossed this region. However, Miller et al. (1986) did not see whales in the Herald Shoal region in 1979 and 1980 during vessel surveys that included the area. Numerous autumn sightings at Herald and Wrangell islands by Siberian natives and a lack of whaling activity in northwest Alaska coastal villages led Braham et al. (1984) to speculate that a northerly route was more likely for many whales. Movements south along the Chukchi Peninsula have been observed through November (Bogoslovskaya et al. 1982), and animals have been seen passing through Bering Strait from mid-October to mid-November (Bessonov et al. 1990). Year-to-year differences likely occur as a result of varying ice and feeding opportunities.

Distances and speeds

This study provides the first details of the routes and rates of movement of many bowhead whales obtained simultaneously. The substantial differences between this study and previous work lie in the durations of individual whale tracks and their speeds. In most cases, these differeces are attributable to the use of different methodologies. Previously, most speed estimates were based on resightings of identifiable bowhead whales (usually by photograpic matching) and were generally confined to coastal regions and made over short periods and short distances. This results in limited numbers of data points for each animal. The rate of travel of satellite-monitored whales (mean = 88 km/d) was higher than the 6–26 km/d estimated for photographically identified bowhead whales by Davis et al. (1983, see footnote 4), Würsig et al. (1983), and Richardson et al. (1987). Only two relocations were obtained over longer distances and times: 749 km in 42 d (18 km/d) and 640 km in 25 d (26 km/d) (Richardson et al. 1987). However, all such distances are minimums and probably dramatically underestimate the movements that may have taken place between sightings. Several photographs of an identifiable whale from the same area over an extended period can also give a mistaken impression of long "residency times," when animals are routinely moving in and out of an area, as right whales do in the Bay of Fundy (Mate et al. 1997).

Conventional very high frequency (VHF) and high-frequency (HF) radio tags have been applied to bowhead whales on three occasions (Table 4). The two studies by Wartzok et al. (1989, see footnote 5, 1990, see footnote 6) involved good ship and aircraft logistics for following tagged whales for long periods, and this resulted in the collection of information on whales that sometimes moved at higher speeds (4.1 km/h for nearly 6 d) for relatively long distances (550 km). East of 145°W, many of our tagged whales stayed in one area for 1–3 d and then moved up to 160 km in a single day (6.7 km/h).

We documented large differences in speed between individual whales but we do not know if these were due to real differences in behavior or to an underestimation of distance for those whales that concentrated their activities in a smaller area. It does not appear that all bowhead whales have a universally favored speed, but some individuals can be quite consistent. The whale with the longest track (DZ-1) moved 12° west in the first 16 d, which included backtracking east and meandering. In contrast, the same whale moved 30° west during the last 16 d, moving consistently west in heavy ice cover. However, the overall average speeds were similar (4.8 vs. 5.1 km/h) for both segments of the track. Superficially, these data suggest that there is no discernible difference in speed during feeding and migration. The limited number of daily locations is more likely to underestimate the true distance and, hence, speed while the whale was meandering in the first segment than during the more linear migratory movements of the second segment.

The average migration speed of the two whales that travelled the farthest west (DZ-1 and D-2, 5.0 and 2.8 km/h, respectively) corresponds roughly to the migration speed of 4 km/h estimated by Rugh (1990). Wartzok et al. (1989, see footnote 5) thought that such speeds were unrealistic, owing to feeding and resting stops, but this may reflect differences between individual whales or in food availability in different years. Moore and Reeves (1993) speculated that it was theoretically possible to move the 1700 km from the Canadian Beaufort Sea to the Russian coast in 18 d at a migration speed of 4 km/h. Whale DZ-1 accomplished this by traveling 2012 km, from 141° to 169°W, in 17.2 d (5 km/h).

Brodie (1981) and Lowry and Frost (1984) modeled filtration factors with whale speeds of 5 and 4.2 km/h, respectively, to estimate the energy budgets of bowhead whales. Our study shows that these are reasonable average speeds for bowhead whales. However, filter-feeding whales must feed where concentrated patches of zooplankton occur (Brodie et al. 1978). Indeed, right whales have been observed to stop and change direction when feeding to stay in the area of highest zooplankton concentration (Winn et al. 1995). Thus, although the tagged bowhead whale traveled at a speed suitable for feeding during its migration, the lack of clustered locations suggests that feeding was not a common activity along the heavy ice edge of the Chukchi Sea.

Influences of ice

Five of the eight satellite-monitored whales in this study encountered ice cover of 50 to >90%. Ice may have influenced the quality and quantity of satellite-acquired locations. Where there are no conspicuous leads, bowhead whales will regularly use the raised region of their blowholes to break through ice that is up to 20 cm thick, and occasionally 60 cm thick, to breathe (George et al. 1989). Usually only a small section of ice rises into a pyramid shape while the whale breathes. Under these circumstances, the whale's body would remain under the ice and our transmitter, not being exposed, would not transmit. In heavy ice, whale locations would most likely have occurred when whales were in leads or pockets of open water. This may explain why there were 45% fewer locations >LC0 during the second half of whale DZ-1's track, when ice cover was heavier, than during the first half.

The track of whale DZ-1 across the Chukchi Sea along the edge of the heavy ice is the only record of bowhead whale movements across this area. The southern edge of the heavy ice across the Chukchi Sea is determined by the warm northward flow of the Anadyr Current from the Bering Strait. This current splits in two, the eastern portion keeping the nearshore waters of the Alaska coast free of ice into the fall and the western (offshore) portion, flowing west of Herald Shoal, slowing the fall advance of the heavy ice front from the north in the central Chukchi Sea and producing a northward intrusion of open water (Springer 1987). It is commonly accepted that the condition of the spring ice affects the timing of the spring migration (Gentleman and Zeh 1987). Ice can also change the surfacing behavior of whales (Würsig et al. 1984). It is not known to what degree the heavy-ice front may be used as a navigation aid or a feeding opportunity by bowhead whales during the fall migration across the Chukchi Sea.

Feeding

The nutritional importance of the Beaufort Sea to bowhead whales has been debated. Schell and Saupe (1993) used stable-isotope ratios from bowhead whale baleen to downplay the importance of bowhead whale summer feeding in the Beaufort Sea. However, feeding is the predominant whale behavior observed in the Beaufort Sea (Würsig et al. 1985). During aerial surveys from 1979 to 1984, Ljungblad et al. (1986) observed 692 instances of bowhead whales feeding from Herschel Island to west of Point Barrow. They estimated that bowhead whales feed for 8–25 d as they migrate west through the Alaskan Beaufort Sea. While Lowry (1993) provides the best overall review of the prey species and feeding ecology of bowhead whales, specific studies provide important background that may explain the bowhead whale movements documented in this tagging study.

In Mackenzie Bay, the location where our whales were tagged, Griffiths and Buchanan (1982) found that copepods were the dominant zooplankton component and that concentrations were higher near whales than in other areas. Bradstreet et al. (1987) reported a high copepod abundance in Mackenzie Bay and estimated that subadult bowhead whales might obtain up to 26% of their annual energy requirements there, in only 6 weeks of feeding. Grainger (1975) determined that the Mackenzie River creates a low-salinity plume in Mackenzie Bay that carries a heavy load of nutrients and particulates. The plume is less distinct farther from shore, as it flows north into the colder, more saline, and generally nutrient-poor Arctic Basin water. Grainger (1975) considered that plankton productivity was low in the plume because of turbidity and low in Arctic Basin water because of low nutrient levels. Thomson et al. (1986) observed that bowhead whales do not usually feed in areas influenced by the plume, yet they suggested that concentrations of bowhead whale food could be produced by several processes: estuarine fronts from the Mackenzie River plume, upwelling off the Yukon coast, turbulence off Herschel Island and Cape Bathurst, and oceanographic phenomena at the shelf break, especially in Mackenzie Canyon. All these locations were areas of high activity (clustered locations) for the bowhead whales tagged in this study. Krutzikowsky and Mate (2000) suggest that two tagged whales that made long, deep dives in Mackenzie Canyon were feeding. Bradstreet et al. (1987) found high zooplankton biomass in areas where southerly or easterly winds caused upwelling in the Arctic Ocean and along subsurface fronts between Arctic Basin water and the Mackenzie plume.

Griffiths et al. (1987) reported that small copepods (*Limnocalanus macrurus*) were the dominant zooplankton component between Demarcation Bay and Barter Island, with the highest concentrations occurring from the shore out to the 50-m contour, and that larger copepods (*Calanus* spp.) were most common offshore. Three of the four tagged whales that used the nearshore areas of Demarcation Bay also used the offshore area. Two whales doubled back and forth through these areas at least twice (DZ-6 (Fig. 8) and DZ-1 (Fig. 10)).

While some "traditionally" productive areas may be feeding areas for bowhead whales, aerial surveys (Ljungblad et al. 1986) show that there are substantial differences in bowhead whale distribution in some years. These differences are likely due to changes in prey distribution associated with shifts in the prevailing winds and the resultant effects on currents and plume patterns (Niebauer 1991).

Lowry and Frost (1984) identified two feeding areas in the Alaska Beaufort Sea: central and western Beaufort Sea. Whales also commonly feed in the eastern (Canadian) Beaufort Sea. An assessment of the Demarcation Bay – Barter Island area in 1985 and 1986 suggested that subadult whales spending 10 d in this area may obtain up to 6% of their annual energy needs (Richardson et al. 1987). Lowry (1993) reported that 13 of 15 whales killed in this area between 1979 and 1988 contained food; of the 11 that were analyzed, most tended to specialize on copepods, euphausiids, or mysids (in order of frequency), but one had had a mixed diet of copepods, amphipods, and euphausiids. Whales DZ-1, DZ-2, DZ-4, and DZ-6 each had a cluster of locations in the Herschel Island or Demarcation Bay regions, and whales DZ-3 and D-1 traveled slowly through these areas. These movements may represent periods of feeding. The tagged-whale data tend to support the claims of local residents that

Demarcation Bay and Herschel Island are important to bowhead whales as staging and (or) feeding areas prior to their westward migration (Braham et al. 1984).

During some years, bowhead whales have fed extensively near Point Barrow (Lowry and Frost 1984; Ljungblad et al. 1986; Moore and Clark 1990; Wartzok et al. 1990, see footnote 6). Analysis of the stomach contents of five of the six bowhead whales killed in the fall at Point Barrow between 1976 and 1988 showed that euphausiids accounted for 96% of their diet (Lowry 1993). There were a cluster of locations for whale DZ-1 in this area, where it may have been feeding.

The route of fall-migrating bowhead whales through the western Beaufort, Chukchi, and Bering seas is likely an important element in bowhead whale feeding strategy. Griffiths et al. (1987) found that euphausiids were the dominant zooplankton species in the central and western Beaufort Sea. Schell and Saupe (1993) reviewed isotopic-ratio data, which differ in the zooplankton communities between the Bering, Chukchi, and Beaufort seas. Schell et al. (1989*a*, 1989*b*) determined that most bowhead whale baleen growth (presumably representing the bulk of nutritional uptake) occurs in the fall and early winter with isotopic signatures most like those of the zooplankton in the Bering, Chukchi, and western Beaufort seas. Primary productivity in the northern Bering Sea is among the highest in the world, owing to long day lengths and advection of nutrient-rich water (Schell and Saupe 1993). The zooplankton community swept north into the central and western Chukchi Sea by the Anadyr Current includes high concentrations of large copepods and juvenile euphausiids (Springer et al. 1989). These populations may peak during the fall bowhead whale migration, possibly influencing both the route and the timing.

Satellite-telemetry technology

Satellite-acquired information has two principal advantages compared with aerial or ship surveys: (1) it gives the simultaneous dynamic movements of individual animals and (2) its coverage is not limited by logistic and political constraints. Its principal advantage over conventional telemetry is that collecting data does not require on-site personnel and costly ships or aircraft (which may also affect whale behavior). These advantages were particularly important in tracking DZ-1 through the Chukchi Sea, where weather, safety, cost, political boundaries, and logistical constraints would have limited how much could have been learned using conventional telemetry or aerial and (or) ship surveys.

The objectives of future experiments will dictate the size, sensors, duty cycle, and repetition rate of future tags. Satellite-monitored tags can be expected to become smaller, more efficient, and less expensive in the future. There will always be a trade-off between more-frequent locations (transmissions) and estimated operational life. Attachment longevity and the effects of cold on batteries remain the two principal problems in long-term tracking of marine Arctic species like the bowhead whale. Despite the large size of whales, it is important to keep surface-mounted tags as small as possible, to reduce hydrodynamic drag.

The utility of various types of sensor data for interpreting whale behavior (see Krutzikowsky and Mate 2000) can be readily appreciated, but adding message length to relay sensor data reduces the number of transmissions possible before batteries become exhausted. Knowledge of the distribution of most large whale species, including the bowhead whale, is limited to approximately one-half of the year. As most whales migrate between summer feeding and winter reproductive areas, there are significant gaps in our understanding of all the areas that constitute their critical habitats. Satellite-monitored radiotelemetry appears to be one of the most cost-effective and useful new tools for discovering these unknown regions. The discovery of seasonally important habitats will help identify stocks, improve population estimates, and promote conservation strategies between countries over species' entire ranges, which are especially important for endangered species. Further, our ability to measure the effects of human activities that may jeopardize whales depends upon a better understanding of the extent of natural variability in whale behavior, seasonal abundance, distribution, and migratory characteristics.

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References

Argos. 1990. User's manual. Service Argos, Landover, Md.

Bessonov, B., Melnikow, V.V., and Bobkov, V.A. 1990. Distribution and migration of cetaceans in the Soviet Chukchi Sea. *In* Proceedings of the 3rd Information Transfer Meeting of the U.S.

Minerals Management Service, Anchorage, 30 January to 1 February 1990, Alaska Outer Continental Shelf Region. pp. 25–31.

Bockstoce, J.R. 1986. Whales, men and ice: the history of whaling in the western Arctic. University of Washington Press, Seattle.

Bockstoce, J.R., and Botkin, D.B. 1983. The historical status and reduction of the western Arctic bowhead whale (*Balaena mysticetus*) population by the pelagic whaling industry, 1848–1914. Rep. Int. Whaling Comm. Spec. Issue No. 5. pp. 107–141.

Bockstoce, J.R., and Burns, J.J. 1993. Commercial whaling in the North Pacific Sector. *In* The bowhead whale. *Edited by* J.J. Burns, J.J. Montague, and C.J. Cowles. Spec. Publ. No. 2, The Society for Marine Mammalogy, Lawrence, Kans. pp. 563–577.

Bogoslovskaya, L.S., Votrogov, L.M., and Krupnik, I.I. 1982. The bowhead whale off Chukotka: migrations and aboriginal whaling. Rep. Int. Whaling Comm. **32**: 391–399.

Bradstreet, M.S.W., Thomson, D.H., and Fissel, D.B. 1987. Zooplankton and bowhead whale feeding in the Canadian Beaufort Sea, 1986. Report by LGL Ltd. to the Canadian Department of Indian Affairs and Northern Development, Ottawa, Ont.

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 Tech. Rep. NMFS SSRF-778.

Brodie, P.F. 1981. A preliminary investigation of the energetics of the bowhead whale (*Balaena mysticetus*). Rep. Int. Whaling Comm. **31**: 501–502.

Brodie, P.F., Sameoto, D.D., and Sheldon, R.W. 1978. Population densities of euphausiids off Nova Scotia as indicated by net samples, whale stomach contents and sonar. Limnol. Oceanogr. **23**: 1264–1267.

Clark, C.W., and Ellison, W.T. 1988. Numbers and distributions of bowhead whales, *Balaena mysticetus*, based on the 1985 acoustic study off Pt. Barrow, Alaska. Rep. Int. Whaling Comm. **38**: 365–370.

Clark, C.W., and Ellison., W.T. 1989. Numbers and distributions of bowhead whales, *Balaena mysticetus*, based on the 1986 acoustic study off Pt. Barrow, Alaska. Rep. Int. Whaling Comm. **39**: 297–303.

Gentleman, R., and Zeh, J.E. 1987. A statistical model for estimating the number of bowhead whales, *Balaena mysticetus*, passing a census point from combined visual and acoustic data. Rep. Int. Whaling Comm. **37**: 313–327.

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

Grainger, E.H. 1975. Biological productivity of the southern Beaufort Sea: the physical–chemical environment and the plankton. Beaufort Sea Tech. Rep. No. 12*a*, Department of the Environment, Victoria, BC V8W 1Y4, Canada.

Griffiths, W.B., and Buchanan, R.A. 1982. Characteristics of bowhead feeding areas. *In* Behavior, disturbance responses and feeding of bowhead whales *Balaena mysticetus* in the Beaufort Sea, 1980–81. *Edited by* W.J. Richardson. Report by LGL Ltd., Toronto, to U.S. Bureau of Land Management, Washington, D.C. NTIS No. PB86-152170, National Technical Information Service, Springfield, Va. pp. 347–355.

Griffiths, W.B., Thomson, D.H., and Johnson, G.E. 1987. Zooplankton and hydroacoustics. *In* Importance of the eastern Alaska Beaufort Sea to feeding bowhead whales, 1985–86. *Edited by* J. Richardson. Report by LGL Ltd., Toronto, to U.S. Minerals Management Service. NTIS No. PB 88 150271/AS, National Technical Information Service, Springfield, Va. pp. 135–256.

Harris, R.B., Fancy, S.G., Douglas, D.C., Garner, G.W., Amstrup, S.C., McCabe, T.R., and Pank, L.F. 1990. Tracking wildlife by satellite: current systems and performance. U.S. Fish Wildl. Serv. Fish. Wildl. Tech. Rep. No. 30.

Keating, K.A., Brewster, W.G., and Key, C.H. 1991. Satellite telemetry: performance of animal-tracking systems. J. Wildl. Manag. **55**: 160–171.

Klinowska, M. 1991. Dolphins, porpoises and whales of the world. The IUCN red data book. International Union for Conservation of Nature and Natural Resources (IUCN), Gland, Switzerland, and Cambridge, U.K.

Koski, W.R., Davis, R.A., Miller, G.W., and Withrow, D.E. 1993. Reproduction. *In* The bowhead whale. *Edited by* J.J. Burns, J.J. Montague, and C.J. Cowles. Spec. Publ. No. 2, The Society for Marine Mammalogy, Lawrence, Kans. pp. 239–274.

Krutzikowsky, G.K., and Mate, B.R. 2000. Dive and surfacing characteristics of bowhead whales (*Balaena mysticetus*) in the Beaufort and Chukchi seas. Can. J. Zool. **78**: 1182–1198.

Ljungblad, D.K., Moore, S.E., and Van Schoik, D.R. 1986. Seasonal patterns of distribution, abundance, migration and behavior of the western Arctic stock of bowhead whales, *Balaena mysticetus*, in Alaskan seas. Rep. Int. Whaling Comm. Spec. Issue No. 8. pp. 177–205.

Ljungblad, D.K., Würsig, B., Swartz, S.L., and Keene, J.M. 1988. Observations on the behavioral responses of bowhead whales (*Balaena mysticetus*) to active geophysical vessels in the Alaskan Beaufort Sea. Arctic, **41**: 183–194.

Lowry, L.F. 1993. Foods and feeding ecology. *In* The bowhead whale. *Edited by* J.J. Burns, J.J. Montague, and C.J. Cowles. Spec. Publ. No. 2, The Society for Marine Mammalogy, Lawrence, Kans. pp. 201–238.

Lowry, L.F., and Frost, K.J. 1984. Foods and feeding of bowhead whales in western and northern Alaska. Sci. Rep. Whales Res. Inst. (Tokyo), **35**: 1–16.

Mate, B.R., Nieukirk, S.L., and Kraus, S.D. 1997. Satellite-monitored movements of the northern right whale. J. Wildl. Manag. **61**: 1393–1405.

Mate, B.R., Gisiner, R., and Mobley, J. 1998. Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry. Can. J. Zool. **76**: 863–868.

Miller, R.V., Rugh, D.J., and Johnson, J.H. 1986. The distribution of bowhead whales, *Balaena mysticetus*, in the Chukchi Sea. Mar. Mamm. Sci. **2**: 214–222.

Montgomery, S. 1987. Report on the 24–26 February workshop to assess possible systems for tracking large cetaceans. NTIS No. PB87-182135, National Technical Information Service, Springfield, Va.

Moore, S.E., and Clarke, J.T. 1990. Distribution, abundance and behavior of endangered whales in the Alaskan Chukchi and Western Beaufort Sea, 1989. Report by SEACO/Science Applications International Corporation to the U.S. Minerals Management Service, Alaska Outer Continental Shelf Region. NTIS No. PB91-105494, National Technical Information Service, Springfield, Va.

Moore, S.E., and Reeves, R.R. 1993. Distribution and movement. *In* The bowhead whale. *Edited by* J.J. Burns, J.J. Montague, and C.J. Cowles. Spec. Publ. No. 2, The Society for Marine Mammalogy, Lawrence, Kans. pp. 313–386.

Niebauer, H.J. 1991. Bio-physical oceanographic interactions at the edge of the Arctic ice pack. J. Mar. Syst. **2**: 209–232.

Richardson, W.J., Würsig, B., and Miller, G.W. 1987. Bowhead distribution, numbers, and activities. *In* Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985–86. *Edited by* W.J. Richardson. Report by LGL Ltd., Toronto, to U.S. Minerals Management Service. NTIS No. PB 150271/AS, National Technical Information Service, Springfield, Va. pp. 257–366.

Rugh, D.J. 1990. Bowhead whales reidentified through aerial photography near Point Barrow, Alaska. Rep. Int. Whaling Comm. Spec. Issue No. 12. pp. 289–294.

Schell, D.M., and Saupe, S.M. 1993. Feeding and growth as indicated by stable isotopes. *In* The bowhead whale. *Edited by* J.J. Burns, J.J. Montague, and C.J. Cowles. Spec. Publ. No. 2, The Society for Marine Mammalogy, Lawrence, Kans. pp. 491–509.

Schell, D.M., Saupe, S.M., and Haubenstock, N. 1989*a*. Natural isotope abundances in bowhead whale (*Balaena mysticetus*) baleen: markers of aging and habitat usage. Ecol. Stud. **68**: 260–269.

Schell, D.M., Saupe, S.M., and Haubenstock, N. 1989*b*. Bowhead whales (*Balaena mysticetus*) growth and feeding as estimated by $\delta^{13}C$ techniques. Mar. Biol. (Berl.), **103**: 433–443.

Springer, A.M. 1987. The paradox of pelagic food webs on the Bering–Chukchi continental shelf. Ph.D. dissertation, University of Alaska Fairbanks, Fairbanks.

Springer, A.M., McRoy, C.P., and Turco, K.R. 1989. The paradox of pelagic food webs in the northern Bering Sea—II. Zooplankton communities. Cont. Shelf Res. **9**: 359–386.

Stewert, B., Leatherwood, S., Yochem, P.K., and Heide-Jorgensen, M.P. 1989. Harbor seal tracking and telemetry by satellite. Mar. Mamm. Sci. **5**: 361–375.

Stoker, S.W., and Krupnik, I.I. 1993. Subsistence whaling. *In* The bowhead whale. *Edited by* J.J. Burns, J.J. Montague, and C.J. Cowles. Spec. Publ. No. 2, The Society for Marine Mammalogy, Lawrence, Kans. pp. 579–629.

Thomson, D.H., Fissel, D.B., Marko, J.R., Davis, R.A., and Borstad, G.A. 1986. Distribution of bowhead whales in relation to hydrometerological events in the Beaufort Sea. Environmental Studies Revolving Funds Rep. No. 028, Canadian Department of Indian Affairs and Northern Development, Ottawa, Ont.

Winn, H.E., Goodyear, J.D., Kenney, R.D., and Petricig, R.O. 1995. Dive patterns of tagged right whales in the Great South Channel. Cont. Shelf Res. **15**: 593–611.

Woodby, D.A., and Botkin, D.B. 1983. Stock sizes prior to commercial whaling. *In* The bowhead whale. *Edited by* J.J. Burns, J.J. Montague, and C.J. Cowles. Spec. Publ. No. 2, The Society for Marine Mammalogy, Lawrence, Kans. pp. 387–407.

Würsig, B., Clark, C.W., Dorsey, E.M., Richardson, W.J., and Wells, R.S. 1983. Normal behavior of bowheads, 1982. *In* Behavior, disturbance responses and distribution of bowhead whales, *Balaena mysticetus*, in the eastern Beaufort Sea, 1982. *Edited by* W.J. Richardson. Report by LGL Ltd., Toronto, to the U.S. Minerals Management Service. NTIS No. PB86-205879/AS, National Technical Information Service, Springfield, Va. pp. 75–115.

Würsig, B., Dorsey, E.M., Fraker, M.A., Payne, R.S., Richardson, W.J., and Wells, R.S. 1984. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: surfacing, respiration, and dive characteristics. Can J. Zool. **62**: 1910–1921.

Würsig, B., Dorsey, E.M., Fraker, M.A., Paine, R.S., and Richardson, W.J. 1985. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: a description. Fish. Bull. **83**: 357–377.

Zeh, J.E., George, J.C., Raftery, A.E., and Carroll, G.E. 1991. Rate of increase, 1978–1988, of bowhead whales, *Balaena mysticetus*, estimated from ice-base census data. Mar. Mamm. Sci. **7**: 105–122.

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* The bowhead whale. *Edited by* J.J. Burns, J.J. Montague, and C.J. Cowles. Spec. Publ. No. 2, The Society for Marine Mammalogy, Lawrence, Kans. pp. 409–489.