Dive and surfacing characteristics of bowhead whales (*Balaena mysticetus*) in the Beaufort and Chukchi seas

Gregory K. Krutzikowsky and Bruce R. Mate

Abstract: We received data from eight bowhead whales (*Balaena mysticetus*) equipped with satellite-monitored radio tags for 3–33 days. Of 42 306 dives made by the eight whales during 1695 h, 9573 were sounding dives (>1 min duration). The mean duration of sounding dives for individuals varied from 6.9 to 14.1 min (mean = 10.4 ± 2.4 min, n = 8). Five whales made dives ≥61 min; the longest dives for the other three lasted 56, 45, and 32 min. Five tags measured maximum depths of 29 499 dives during 1220 h and time at depth during 1228 h. All five whales dived >100 m; the deepest dive was 352 m. Whales spent most of their time at depths ≤16 m, but three whales spent most of their time at depths >48 m during some sampling periods. Mean surfacing rates ranged from 18.2 to 47.0/h (mean = 26.2 ± 9.0/h, n = 8). Tags were exposed to air for 4.0–7.3% of the time (mean = 5.5 ± 0.95%, n = 8), and whales were potentially visible from aircraft for 8.5–16.4% of the time (mean = 11.1 ± 2.4%, n = 8). Three whales made longer sounding dives and had lower surfacing rates when in ≥90% ice cover. No consistent diel patterns were found.

Résumé : Nous avons reçu des données sur huit Baleines boréales (*Balaena mysticetus*) munies d'émetteurs-radio contrôlés par satellite durant une période de 3 à 33 jours. De 42 306 plongées faites par huit baleines au cours de 1695 h, 9573 étaient des plongées d'exploration (>1 min). La durée moyenne des plongées d'exploration allait de 6,9 à 14,1 min (la moyenne = 10,4 ± 2,4 min, n = 8). Cinq des baleines ont fait des plongées de ≥61 min et les plongées les plus longues enregistrées chez les trois autres ont duré 56, 45 et 32 min. Cinq marqueurs ont mesuré les profondeurs maximales de 29 499 plongées au cours d'une période de 1220 h et mesuré le temps passé aux différentes profondeurs durant 1228 h. Les cinq baleines ont plongé à plus de 100 m; la plus grande profondeur atteinte au cours d'une plongée a été de 352 m. Les baleines ont passé la plus grande partie de leur temps à des profondeurs de ≤16 m, mais trois d'entre elles sont restées à plus de 48 m au cours de certaines périodes. Les taux moyens de retour en surface allaient de 18,2 à 47,0/h (la moyenne = 26,2 ± 9,0/h, n = 8). Les marqueurs ont été exposés à l'air de 4,0 à 7,3 % du temps (la moyenne = 5,5 ± 0,95 %, n = 8) et les baleines pouvaient être vues d'un aéronef de 8,5 à 16,4 % du temps (la moyenne = 11,1 ± 2,4 %, n = 8). Trois baleines ont fait des plongées exploratoires plus longues et elles avaient des taux de retour en surface moins importants lorsque la couverture de glace était de ≥90 %. Nous n'avons pas trouvé de patterns quotidiens bien définis.

[Traduit par la Rédaction]

Introduction

Until recently, researchers were unable to investigate the dive and surfacing behavior of cetaceans in the wild unless individual animals were readily visible and identifiable. The advent of microprocessor-controlled data loggers linked with miniature satellite radiotelemetry equipment has helped to change this situation. Data can now be gathered around the clock on free-ranging cetaceans worldwide (e.g., Martin and Smith 1992; Mate et al. 1994, 1995; Martin et al. 1994; Heide-Jørgensen and Dietz 1995; Davis et al. 1996). Here we present the first satellite-monitored radiotelemetry data on the dive and surfacing characteristics of bowhead whales (*Balaena mysticetus*) in waters that seasonally host (Moore and Reeves 1993) the largest remaining population of this species (Zeh et al. 1993).

Although this endangered species (Klinowska 1991) is no longer hunted commercially, subsistence hunting of the Bering Sea stock continues (Stoker and Krupnik 1993). Concern about whether other human activities such as mineral exploitation, shipping, and pollution threaten this population have led to numerous studies of bowhead whales in the Beaufort and Chukchi seas (Montague 1993). Studies of the surfacing and diving habits of bowhead whales provide information that is useful to management agencies, as well as clues for interpreting whale behavior. Dive, surfacing, and respiration patterns are used to calculate detection probabilities, to estimate the proportion of time whales are visible from the air (Carroll and Smithhisler 1980; Würsig et al. 1984; Dorsey et al. 1989; Zeh et al. 1993), and to adjust abundance estimates from survey data (Davis et al. 1982;

Received August 10, 1999. Accepted February 16, 2000.

G.K. Krutzikowsky.[1] Oregon State University, College of Oceanic and Atmospheric Sciences, Hatfield Marine Science Center, Newport, OR 97365, U.S.A.
B.R. Mate. Oregon State University, Department of Fisheries and Wildlife, Coastal Oregon Marine Experiment Station, Hatfield Marine Science Center, Newport, OR 97365, U.S.A.

[1]Author to whom all correspondence should be sent at the following address: Oregon State University, Cooperative Institute for Marine Resource Studies, Hatfield Marine Science Center, Newport, OR 97365, U.S.A. (e-mail: greg.krutz@hmsc.orst.edu).

Table 1. Data collected by satellite-monitored radio tags deployed on bowhead whales in 1992.

Tag No.	Date tagged	Date first data received	Date last data received	No. of sampling periods: Duration[a]	Depth[b]	TAD[c]	Locations
D-1	6 Sept.	5–6 Sept.	5–29 Sept.	33	—	—	9
D-2	6 Sept.	3–6 Sept.	5–22 Sept.	49	—	—	13
DZ-1	2 Sept.	1–3 Sept.	2–5 Oct.	222	220	223	136
DZ-2	2 Sept.	3–3 Sept.	7–10 Sept.	42	44	46	18
DZ-3	5 Sept.	8–5 Sept.	6–8 Sept.	19	12	15	5
DZ-4	3 Sept.	8–3 Sept.	6–14 Sept.	78	76	78	52
DZ-5	3 Sept.	1–4 Sept.	7–12 Sept.	59	55[d]	53[d]	28
DZ-6	4 Sept.	1–5 Sept.	6–14 Sept.	63	58	54	30

[a] D tags reported the number of dives in eight duration categories: 0–1 (±3.5), 1–4, 4–7, 7–10, 10–13, 13–16, 16–19, and >19 min; the longest dive (13–71 ± 1 min); the longest surfacing (1.5–30.5 ± 0.5 min); and total time spent under water (68.4–180.0 ± 0.9 min). DZ tags reported the number of dives in nine duration categories: 0–1 (±4), 1–4, 4–7, 7–10, 10–13, 13–16, 16–19, 19–25, and >25 min; the longest dive (0–60 ± 1 min); and the duration of the first dive to the maximum depth (0–60 ± 1 min).

[b] DZ tags reported the number of dives in eight depth categories: 0–16 (±1), 17–32 (±1), 33–48, 49–96, 96–200, 200–400, 400–800, and >800 m; and the deepest dive (0–1024 ± 8 m).

[c] Time at depth. DZ tags reported time spent in eight depth categories (±1.8 min): 0–16, 16–32, 32–48, 48–96, 96–200, 200–400, 400–800, and >800 m; the longest surfacing (0–62 ± 0.5 min); and total time spent at the surface (0–126 ± 0.5 min).

[d] The depth sensor for this tag was faulty. Only the total numbers of dives and surface times were used from the depth and TAD packets.

Hiby and Hammond 1989). Respiration rates are used to estimate energetic budgets (Thomson 1987). Factors that may affect the diving and surfacing behavior of undisturbed bowhead whales have been investigated (Würsig et al. 1984; Dorsey et al. 1989), and changes in these behaviors are used as a measure of disturbance by vessel, industrial, and seismic activity (Richardson et al. 1985, 1986; Ljungblad et al. 1988). Despite study of their dive durations and surfacing behavior, little is known about the depths to which bowhead whales dive, where in the water column they spend their time, or their nighttime activity.

Methods

We equipped 12 bowhead whales with satellite-monitored radio tags near Shingle Point, Northwest Territories, Canada (68°59′N, 137°26′W), between 30 August and 6 September 1992 (Table 1). Mate et al. (2000) describe the physical details of the tags and deployment methods. We placed tags close to the middorsal line approximately 3 m behind the blowhole, to ensure tag and antenna exposure during surfacings. All whales tagged were of unknown sex and were estimated to be juveniles or subadults (Koski et al. 1993) between 8 and 12 m in length. Two types of tags were deployed: those that recorded depth and duration information (DZ tags, n = 10) and those that collected only duration information (D tags, n = 2). Data and calculated locations for tags were obtained using the Argos data collection and location system (ADCLS) (Harris et al. 1990). Movements of individual whales and screening of Argos locations are described in the companion paper (Mate et al. 2000). This paper reports dive and surfacing data for eight whales (two D tags and six DZ tags) for which we obtained both location and sensor information.

Each tag collected sensor information during a sampling period and stored 64-bit information “packets” for transmission at a later time. To detect transmission errors, a cyclic redundancy check code was included with each packet (Lin 1970; Wakerly 1978). For each sampling period, D tags collected one packet that included the number of dives in each of eight duration categories or bins, duration of the longest dive, duration of the longest surfacing, and total time spent under water (Table 1). DZ tags collected three packets for each sampling period (Table 1). The duration packet included the number of dives in each of nine duration bins, duration of the longest dive, and duration of the first dive to the maximum depth. Each dive was assigned to one of eight depth bins, based on its maximum depth. The depth packet included the number of dives in each of eight depth bins and the maximum depth reached. The time-at-depth (TAD) packet included the time spent in each of eight depth bins, total surface time, and duration of the longest surfacing. Maximum and minimum values were established for each transmission field. If data fell outside the range of specified values, they were recorded as underflow or overflow values. For example, D tags reported an underflow if the longest dive in the period lasted <12 min and an overflow if it lasted ≥72 min (Table 1). Data were checked for logical consistency and only valid sensor information was retained.

Times and dates are reported in universal coordinated time (UTC). D tags sampled according to our experimental design: eight 3-h sampling periods beginning at 00:00 UTC each day. The D-tag duty cycle allowed transmissions during the first 100 min of each 12 h. Transmissions rotated through data packets from the previous four sampling periods. A software error in the DZ tags resulted in one 1-h sampling period, six 3-h sampling periods, and one 5-h sampling period, beginning at 02:00 UTC each day. DZ tags could transmit at any time of day. DZ-tag transmissions included four of the six data packets from the two previously completed sampling periods on a rotating basis. All tags were limited to transmitting once every 40 s.

Dive and surface durations were measured by sampling conductivity between the tag housing and a salt-water switch, to determine if the tag was submerged. We defined a dive as a submergence lasting >6 s. A pressure transducer in the DZ tags measured ambient pressure and registered the equivalent depth of seawater in 8-m increments. D tags interrogated the salt-water switch every 0.25 s to determine if the tag was submerged, but tallied time in 2-s intervals. DZ tags tallied time in 6-s intervals but interrogated the salt-water switch and pressure transducer at various intervals: 0.25 s while at depths <8 m, 1 s while at depths of 8–32 m, and 6 s while at depths >32 m. This was done to conserve battery power during dives, while ensuring that surfacings were detected.

Tags reported short dives (≤1 min) in multiples of either four (DZ tags) or eight (D tags) and shallow dives (≤32 m) in multiples of two (Table 1). If DZ tags returned both duration- and depth-packet data for a sampling period, we compared the minimum and maximum number of dives in each packet to determine the smallest possible range of values. For all tags, the number of dives in the first duration bin was taken to be the mean of the minimum and maximum number of dives possible in that bin during the period. Any uncertainty in the number of dives in the first two depth bins was spread equally between them, resulting in fractional total dive counts. For D tags, the total number of dives in a period was always ±3.5. For DZ tags, the total number of dives was the exact number in 91 sampling periods, ±0.5 in 215 sampling periods, ±1.0 in 177 sampling periods, and ±1.5 in 28 sampling periods. Surfacing rate (surfacings/h) for the sampling period was defined as the total number of dives divided by the period length.

We considered dives >1 min long to be sounding dives. To characterize sounding dives for each period and to make statistical comparisons, we collapsed the duration data for each sampling period into one variable, average duration of sounding dives (SDUR):

$$[1]\quad \text{SDUR} = \Sigma\,(\text{number of dives in the duration bin} \times \text{midpoint of the bin})/(\text{total number of sounding dives})$$

For dives in the longest bin, the duration of the longest dive (and the first dive to the maximum depth for DZ tags) was known and used in the calculation. Subsequent dives in this bin were multiplied by the midpoint between the longest dive and the bin's minimum value. Sampling periods with overflow values for the longest dive were excluded from these analyses.

We calculated the proportion of each sampling period that tagged animals were potentially visible from the air:

$$[2]\quad \text{percentage of time potentially visible} = 100\,[\text{surface time} + 10\,(\text{dr1})]/\text{period length}$$

where dr1 is the number of dives ≤1 min and both surface time and period length are in seconds. We assumed (*i*) that whales were visible during the surface time tags recorded, (*ii*) that dives ≤1 min were series dives during a surfacing sequence, and (*iii*) that whales were visible during these series dives but not before or after them. The number of dives ≤1 min was multiplied by 10 s, the mean time spent under water between blows measured during three ice-based visual studies of bowhead whale behavior (Carroll and Smithhisler 1980; Rugh and Cubbage 1980; Zeh et al. 1993).

Water depths at Argos locations were determined from National Oceanic and Atmospheric Administration chart No. 16003 or U.S. Defense Mapping Agency chart No. 15026. Ice-cover conditions near whale locations were 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. For each whale, approximate daily sunrise and sunset times (UTC) were determined according to date, Argos locations, and published sunrise and sunset information (U.S. Department of Commerce 1991). Sampling periods were assigned to one of four classifications to indicate time of day: (1) night, if they began more than 1 h after local sunset and ended more than 1 h before local sunrise; (2) dawn, if sunrise occurred either during the period or within 1 h of the end of the period; (3) day, if they began and ended between sunrise and sunset; and (4) dusk, if sunset occurred either during the period or within 1 h of when the period began. Because so few dawn and dusk periods were recorded for each animal, they were combined into a twilight category for statistical tests.

To determine whether the length of the sampling period affected the data collected by DZ tags, we used multiple linear regression analysis allowing for differences among the whales[2] (Ramsey and Schafer 1996). Because all 1- and 5-h periods occurred during daylight, we included only 3-h periods that occurred during daylight in this analysis. Data for sampling periods when the duration of either the longest dive or the first dive to the maximum depth overflowed were excluded from this analysis.

Sampling-period length did not affect the surfacing rate, the percentage of the period spent at the surface, the percentage of time the whale was potentially visible from the air, SDUR, the duration of the first dive to the maximum depth, or the maximum depth reached for any of the DZ tags. Therefore, sampling periods were treated equally in subsequent statistical comparisons of these variables. However, the longest dive recorded in a sampling period increased when sampling occurred over a longer time. The effects of differences in period length were similar for all tags. Consequently, we compared longest dives for sampling periods of equal length.

Statistical comparisons were accomplished with parametric tests when possible. Data were logarithmically transformed where appropriate and geometric-mean values with 95% confidence intervals (CI) subsequently reported. Visual observation of residual plots and (or) the Kolmogorov–Smirnoff test for normality were used to determine if parametric tests were appropriate. When outliers were present, analyses were done both with and without the outliers, to determine the sensitivity of the analysis to their presence. Between-group differences in means for analysis of variance (ANOVA) tests were accomplished with the Fisher's protected least significant difference (LSD) technique. Nonparametric tests were used to compare medians, if data included underflow–overflow values or data transformations failed to meet the assumptions required for parametric tests. The significance level for all tests was set at 0.05 unless otherwide indicated. The Statgraphics Plus® (Manugistics Inc., Rockville, Md.) statistical software package was used in data analysis.

Results

Dive durations

The distribution of dive durations was highly skewed for every animal, 64–83% of dives lasting ≤1 min (Fig. 1). Overall, 77% of the 42 306 dives made by the eight whales during 1695 h lasted ≤1 min, leaving 9573 sounding dives. Most whales exhibited a general decline in the number of sounding dives of successively longer durations, with notable exceptions from three whales who recorded the highest percentages of sounding dives at 13–19 min (DZ-2) or 10–

[2] Dependent variables were substituted into the equation

$$\text{dependent variable} = \beta_0 + \beta_1(\text{period length}) + \beta_2(\text{DZ-2}) + \beta_3(\text{DZ-3}) + \beta_4(\text{DZ-4}) + \beta_5(\text{DZ-5}) + \beta_6(\text{DZ-6}) + \beta_7(\text{period length})(\text{DZ-2}) + \beta_8(\text{period length})(\text{DZ-3}) + \beta_9(\text{period length})(\text{DZ-4}) + \beta_{10}(\text{period length})(\text{DZ-5}) + \beta_{11}(\text{period length})(\text{DZ-6})$$

Period lengths were 1, 3, and 5 h. Tag DZ-1 was used as the standard and other tags (DZ-2 through DZ-6) were put into the equation as indicator variables (1 or 0) to allow for differences among tags. Interaction terms, multiples of period length and tag indicator, tested for differences in the effect of period length by tag. The t value and associated p value for each coefficient, β_i, in the equation determined the significance of that factor in the model.

Fig. 1. Relative frequency of dives recorded in each duration category by satellite-monitored radio tags deployed on eight bowhead whales in 1992; *n* is the number of dives.

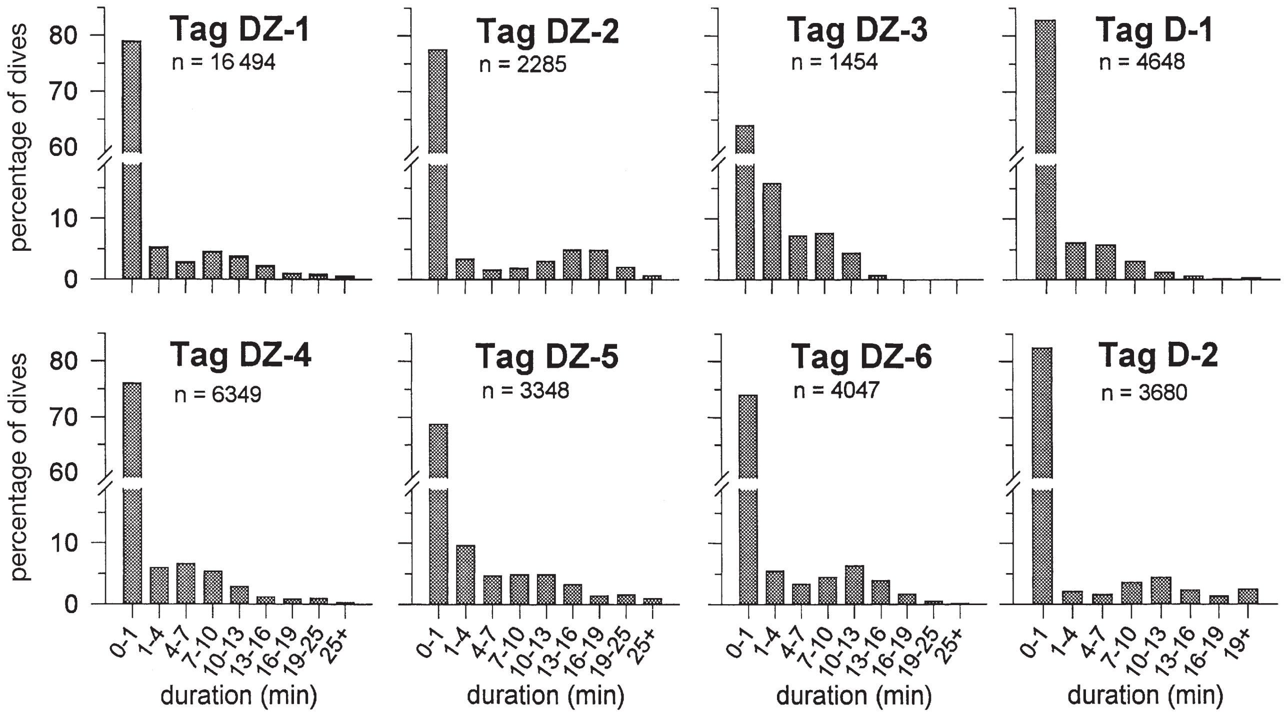
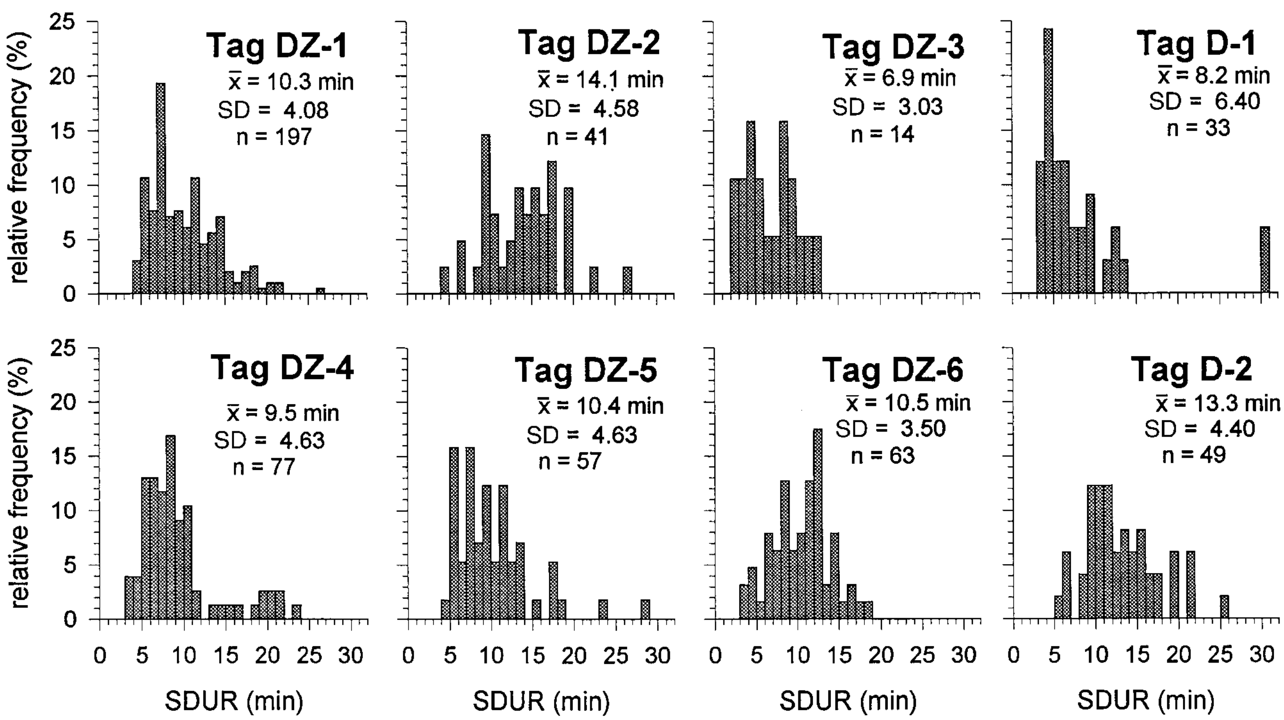


Fig. 2. Relative frequency of average duration of sounding dives (SDUR) during the sampling period for eight bowhead whales equipped with satellite-monitored radio tags; *n* is the number of sampling periods. See the text for calculation of SDUR.



13 min (DZ-6 and D-2) (Fig. 1). SDUR ranged from 2.6 to 30.4 min (n = 536). Mean SDUR for individuals varied from 6.9 ± 3.0 to 14.1 ± 4.6 min (mean = 10.4 ± 2.4 min, n = 8), and six of the eight whales exhibited a range of 20 min or more across sampling periods (Fig. 2).

Five of the eight tags reported being submerged for at least 61 min, and the longest dives for the other three whales were 56, 45, and 32 min (Fig. 3). The longest dive of known duration, reported by tag D-1, lasted between 62 and 64 min. However, longer dives may have occurred in the 29 sam-

Fig. 3. Relative frequency of the longest dives recorded in a sampling period by eight satellite-monitored radio tags deployed on bowhead whales. Open bars represent underflow or overflow values; *n* is the number of sampling periods.

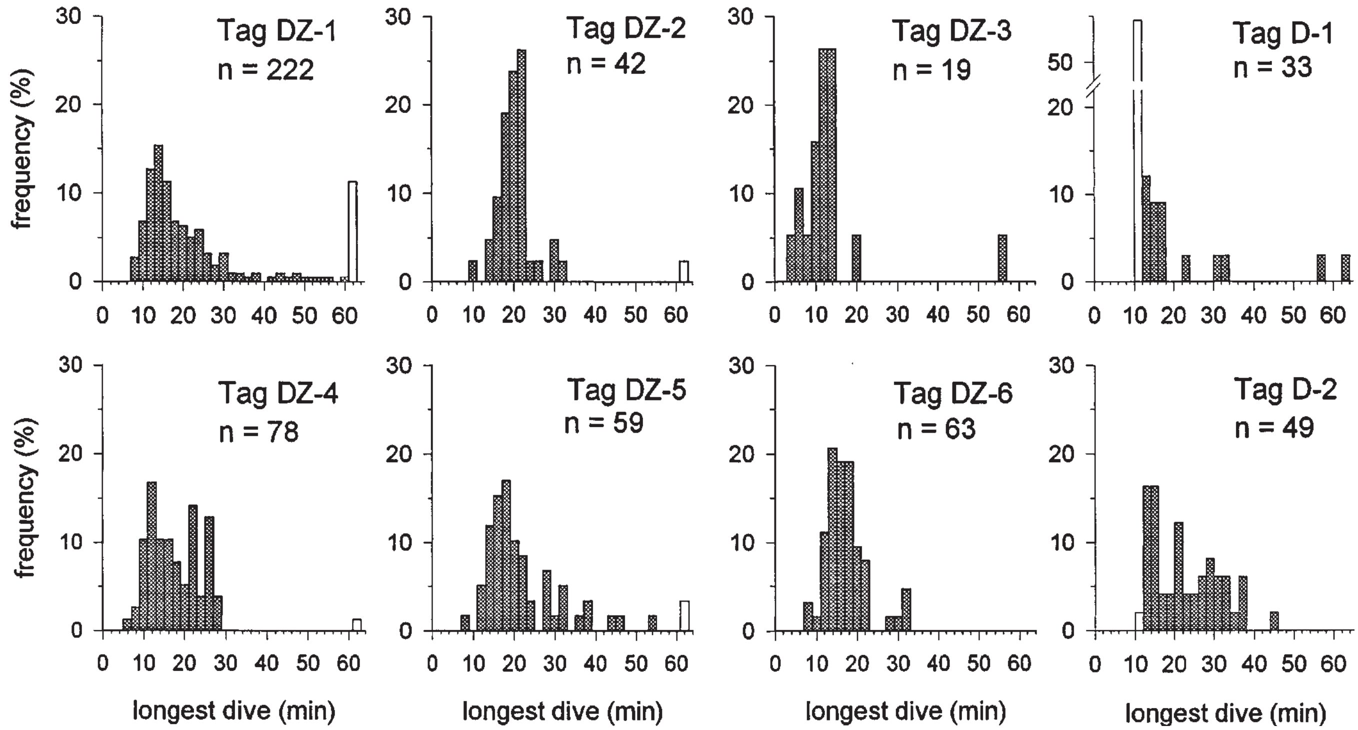
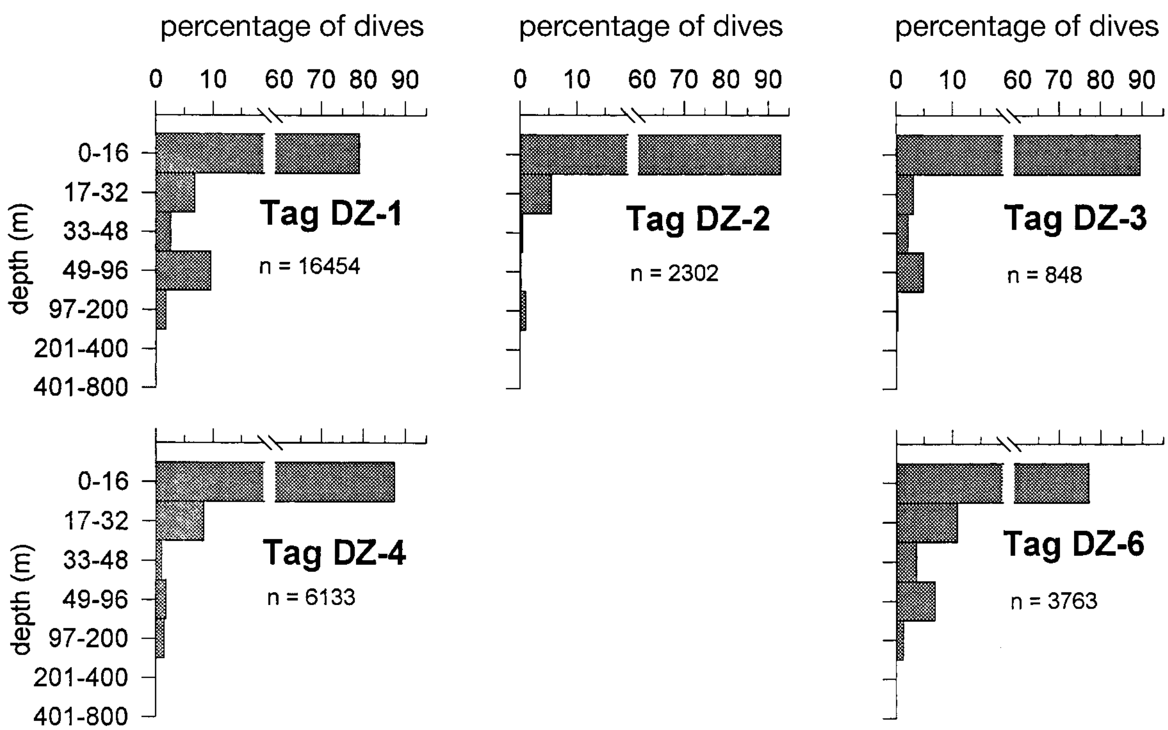


Fig. 4. Relative frequency of the maximum depths of dives recorded by satellite-monitored radio tags deployed on five bowhead whales; *n* is the number of dives.



pling periods during which DZ tags reported dives ≥61 min (overflow value). Most of the dives ≥61 min long occurred in ice cover ≥90%, but tags DZ-1, DZ-2, and DZ-4 recorded dives this long in open water.

Dive depth and TAD

Maximum depths of 29 499 dives made by five whales with DZ tags were measured during 1220 h. Dives ≤16 m accounted for 77–93% of the total number of dives for each

Fig. 5. Percentages of time recorded in each depth category for five bowhead whales equipped with satellite-monitored radio tags; *n* is the number of hours that TAD was monitored.

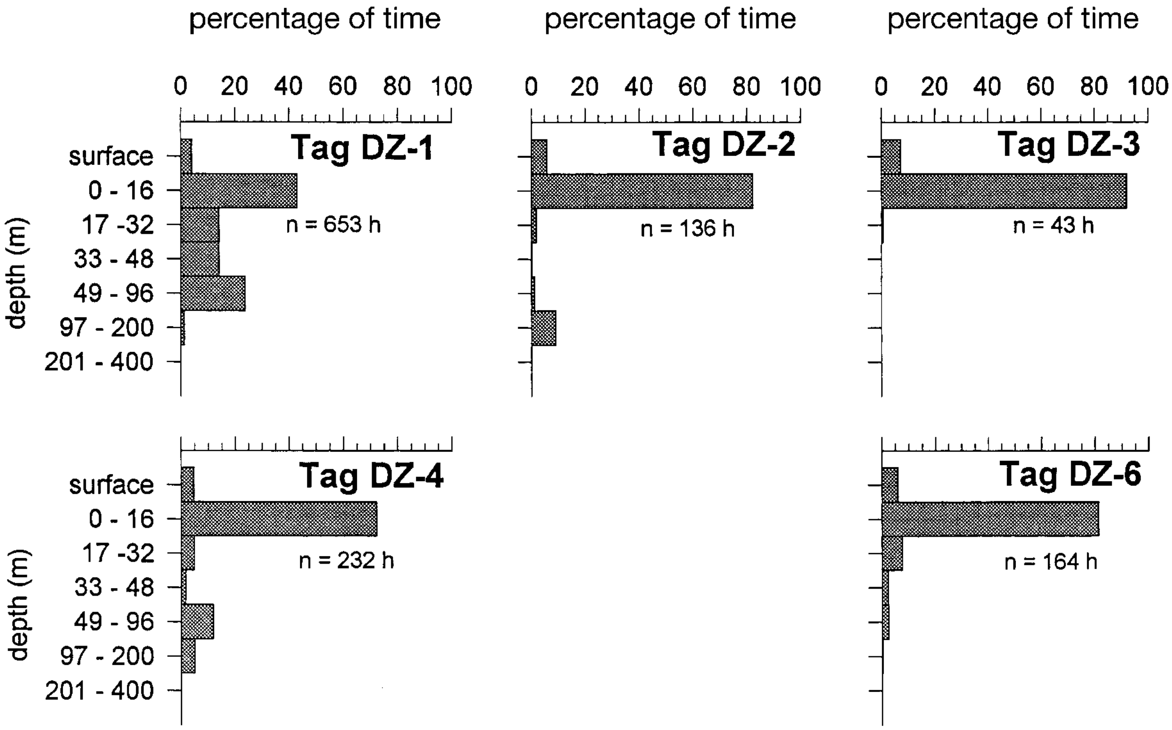


Table 2. Data for the deepest dive during sampling periods recorded by satelite-monitored radio tags on bowhead whales.

		Deepest dive (m)				
Tag No.	*n*	Minimum	Mode	Median	Mean ± SD	Maximum
DZ-1	220	32	96	96	97±41	352
DZ-2	44	<8	32	32	38±34	160
DZ-3	12	<8	<8	56	52±49	128
DZ-4	76	16	32	48	63±43	160
DZ-6	58	16	96	88	84±40	240

whale (Fig. 4). Maximum depth reached during a sampling period ranged from <8 to 352 m and all five whales made dives >100 m deep (Table 2). Several tagged whales exhibited bouts of repeated dives ≥48 m deep.

Overall, during 1228 h, the five whales spent 60% between the surface and 16 m depth, 33% between 17 and 96 m depth, and <3% at depths greater than 96 m, the remainder being spent at the surface. Every whale spent most of its time between the surface and 16 m depth (Fig. 5). However, three individuals (DZ-1, DZ-2, and DZ-4) spent more than half of some periods at depths greater than 48 m.

Relationship between dive depth and duration

The number of short (≤1 min) dives and the number of shallow (≤16 m) dives recorded in a sampling period by DZ tags were positively correlated (r = 0.95–0.97, all $p < 0.0001$). Thus, the short series dives during a surfacing sequence were probably shallow.

The duration of the first dive to the maximum depth ranged from <1 to ≥61 min (n = 415). Four tags reported the underflow value (<1 min) for this dive in 21 periods. Depth data were reported in 17 of these 21 periods. The deepest dive was <8 m in five of these periods, 8–16 m in seven periods, and 17–32 m in the other five periods. Considering the close association between short and shallow dives, it seems likely that the first dive to the maximum depth recorded during these periods was one of the short series dives during a surfacing sequence. Three tags reported that the first dive to the maximum depth was ≥61 min long (overflow value) in 15 sampling periods, with dive depths ranging from 16 to 128 m. Of these 15 periods, 12 were recorded by tag DZ-1 in heavy ice conditions. Sampling periods with underflow or overflow values were excluded from further analyses. The first dive to the maximum depth was also the longest dive in 105 of the 367 sampling periods for which the duration of both was known.

To investigate the relationship between duration and depth of the first dive to the maximum depth, a regression analysis was performed on data from each of the five tags. Duration significantly increased with dive depth for four of the five whales, but the linear model explained <36% of the variation around the mean in all cases (Fig. 6). One outlier value

Fig. 6. Results of regression of duration on depth for the first dive in a sampling period to reach the maximum depth recorded in the period for five bowhead whales equipped with satellite-monitored radio tags.

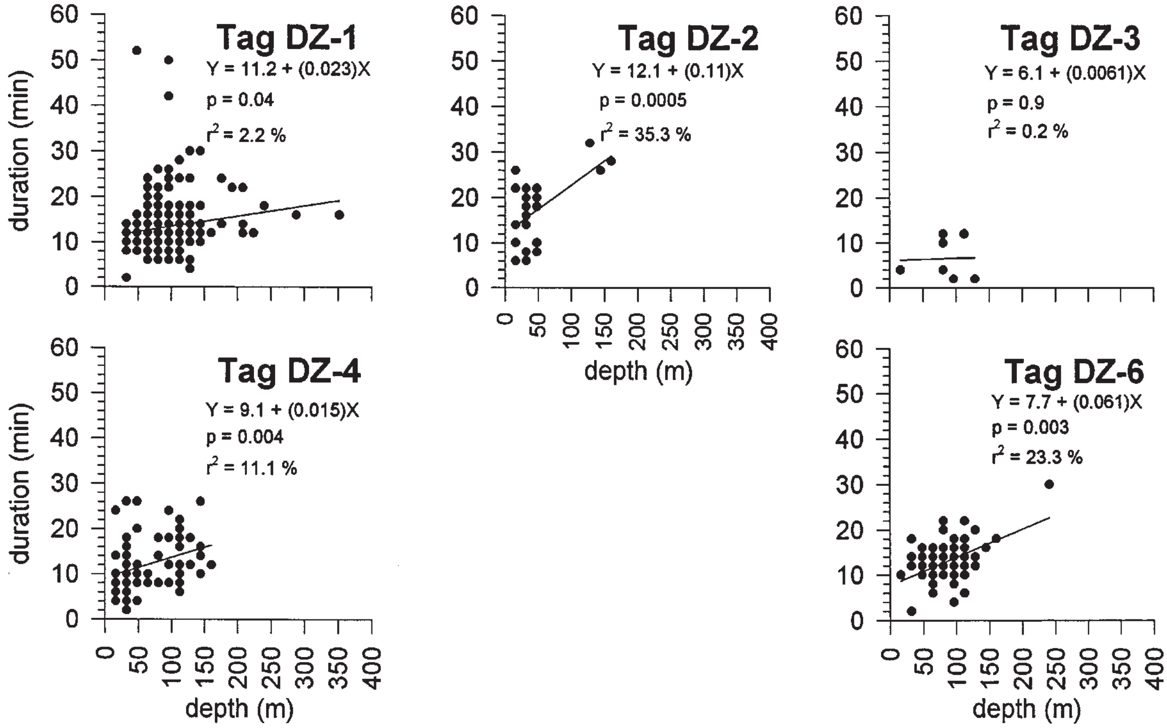


Table 3. Surfacing rate, percentage of time spent at the surface, and percentage of time potentially visible from the air for bowhead whales tagged in 1992.

Tag No.	No. of surfacings/h	Percentage of surface time	Percentage of time potentially visible from the air
DZ-1	25.1±10.8 (229)	4.0±2.04 (223)	9.5±3.0 (214)
DZ-2	18.2±6.5 (45)	5.9±2.02 (46)	10.0±2.3 (40)
DZ-3	25.5±13.3 (19)	7.3±4.32 (16)	12.5±5.8 (15)
DZ-4	26.9±7.3 (79)	4.7±4.36 (78)	10.2±4.4 (78)
DZ-5	18.9±7.9 (63)	4.8±3.27 (54)	8.5±3.6 (51)
DZ-6	22.9±17.5 (68)	6.1±2.67 (61)	10.7±5.2 (59)
D-1	47.0±20.6 (33)	5.7±2.35 (33)	16.4±5.9 (33)
D-2	25.0±12.0 (49)	5.6±1.89 (49)	11.3±2.4 (49)
Mean	26.2±9.0 (8)	5.5±0.95 (8)	11.1±2.4 (8)

Note: Values are given as the mean ± SD, with the sample size in parentheses.

strongly influenced the analysis for tag DZ-6 (Fig. 6), but the positive relationship remained if the outlier was excluded from the analysis (p = 0.03).

Surfacings

Both types of tags recorded the longest surfacing duration in each sampling period. Four of the eight whales reported surfacings of longer than 3.5 min. These long surfacings occurred in only 5 of the 560 sampling periods and were approximately 14, 8, 5, 4, and 4 min long.

Individual whales exposed their tags to the air for an average of 4.0–7.3% of the sampling period (Table 3). This translates to exposure at the surface for between 2.4 and 4.4 min/h. Mean rates for individuals ranged from 18.2 to 47.0 surfacings/h (Table 3). Based on the calculations in eq. 2, the mean percentage of the sampling period potentially visible from the air for individuals ranged from 8.5 to 16.4% (Table 3).

Dive and surfacing characteristics in relation to location and environment

Detailed location data for tagged bowhead whales are presented and discussed in the companion paper (Mate et al. 2000). Argos locations were obtained for whales in 291 sampling periods, with individual whales located during 9–136 periods (Table 1). Here we examine aspects of dive and surfacing data in relation to ice cover and time of day. We also note similarities among three whales that were located in Mackenzie Canyon at about the same time.

Ice cover

Five of the eight whales moved into waters with various degrees of ice cover, but only three were monitored in areas with heavy ice cover ≥90% (Mate et al. 2000). Whale D-1 was surrounded by ≥90% ice cover at its last location just north of the Mackenzie River Delta on 29 September (see Fig. 4 in Mate et al. 2000). Late on 20 September, at its most westerly location (see Fig. 9 in Mate et al. 2000), whale D-2 was surrounded by 90% ice cover. From 20 September until 5 October, when it was last heard from, whale DZ-1 migrated through water with ice cover ≥90% (see Fig. 10 in Mate et al. 2000). These animals exhibited consistent differences in several dive and surfacing variables when they were in heavy (≥90%) versus lighter (<90%) ice cover (Table 4). All three had lower surfacing rates, yet recorded more time at the surface. Although surface time increased, the calculated percentage of time they were potentially visible from the air declined because of the lower surfacing rate. The longest surfacing increased for two of the three whales. Average sounding dive time increased for all three whales, as did the duration of their longest dives. These differences were significant, except for the percentage of time spent at the surface for whales D-1 and D-2, where the power to detect a difference was low, owing to the small sample sizes in heavy ice.

When in heavy ice conditions, whale DZ-1 made longer dives (Fig. 7A), made a higher percentage of dives to depths of >48 m (Fig. 7B), spent more of its time at depths of 49–96 m, and spent less time between 0 and 16 m depth (Fig. 7C). These differences were not simply a function of available water depth. Dive-depth data were received for 56 periods, with locations in water >48 m deep being evenly split between heavy and lighter ice conditions. The percentages of dives ≤16 m deep were nearly identical in the two samples, 77 and 78% in heavy and lighter ice, respectively, but 20% of the dives were to depths of >48 m in heavy ice versus 12% in lighter ice. TAD data were received from 53 sampling periods with locations in water >48 m deep. Although water depths at locations in the 26 periods in light ice ranged up to 1480 m, whale DZ-1 spent 58% of its time in the upper 16 m and 14% of its time at depths of 49–96 m. In contrast, during the 27 periods in heavy ice, water depths ranged only up to 128 m, yet this whale spent most of its time (55%) between 48 and 96 m, with only 22% of its time in the upper 16 m. The tag did not break the surface during four 1-h sampling periods recorded after 19 September. TAD information for these periods hints that surfacing behavior still occurred. Although this whale spent most of its time in these periods at depths of >32 m (mean = 71.8 ± 9.8%), it still spent substantial time in the upper 16 m (mean = 25.8 ± 11.0%); however, it spent very little time in between (mean = 3.0 ± 5.2% at 17–32 m).

Diel variation

To investigate diel patterns of behavior for each whale, we compared data recorded during day, night, and twilight periods for six variables: surfacing rate, percentage of time spent at the surface, duration of the longest dive, logarithmically

Table 4. Comparison of dive and surfacing variables between three bowhead whales in heavy (≥90%) versus lighter (<90%) ice cover.

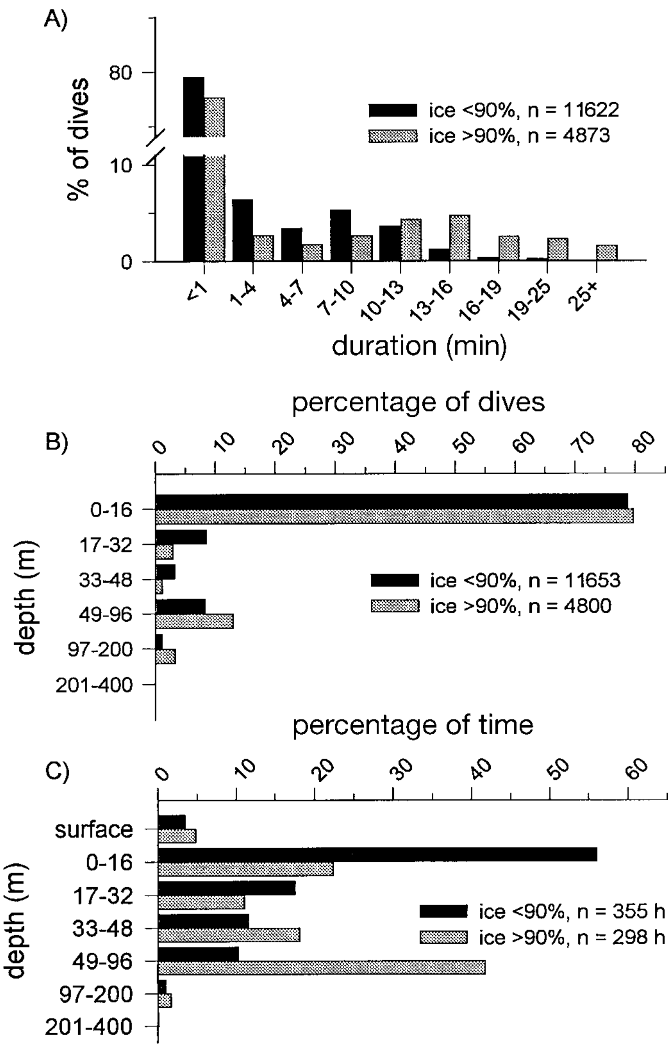
	Surfacing rate (no. of surfacings/h)		Surface time (%)		Longest surfacing (min)		Time potentially visible from the air (%)		SDUR (min)		Longest dives 1-h periods		Longest dives 3-h periods		Longest dives 5-h periods	
	<90%	≥90%	<90%	≥90%	<90%	≥90%	<90%	≥90%	<90%	≥90%	<90%	≥90%	<90%	≥90%	<90%	≥90%
D-1[a]	47.8	11.8***	4.5	5.5	<1	<1	16.8	8.0***	5.7	30.4***			<12	57***		
	(30)	(3)	(30)	(3)	(30)	(3)	(30)	(3)	(30)	(3)			(30)	(3)		
D-2[a]	27.5	8.5**	5.5	6.5	<1	1–2***	11.5	8.3***	11.7	19.1**			21	28*		
	(45)	(4)	(45)	(4)	(45)	(4)	(45)	(4)	(45)	(4)			(45)	(4)		
DZ-1[b]	32.1±6.8	16.3±8.0***	3.3	4.9***	<0.5	0.5–1.5***	9.1	10.4***	7.7	13.2***	11.1	17.8***	14.7	24.7***	17.2	22.9*
	(128)	(101)	(121)	(102)	(121)	(102)	(117)	(97)	(120)	(77)	(15)	(9)	(91)	(61)	(14)	(7)

Note: Data are from satellite-monitored radio tags. Numbers in parentheses are sample sizes. A significant difference from lighter ice is indicated as follows: *, $p < 0.1$; **, $p < 0.05$; ***, $p < 0.005$. We considered differences to be significant in two cases with $0.1 < p < 0.05$ because of the small sample sizes and subsequent low power to detect differences.

[a]Medians are given for all variables.

[b]Mean and SD are given for surfacing rates. Medians are given for surface time, longest surfacing, time potentially visible from the air, and longest dives. Geometric means are given for SDUR.

Fig. 7. Comparison of dive data recorded by satellite-monitored radio tag DZ-1 on a bowhead whale in light ice (<90%) from 3 to 19 September 1992 and in heavy ice (≥90%) from 20 September to 5 October 1992. (A) Percentage of dives in each duration category; *n* is the number of dives recorded. (B) Percentage of dives in each depth category; *n* is the number of dives recorded. (C) Percentage of time spent in each depth category; *n* is the number of hours of monitoring.



transformed SDUR, deepest dive, and duration of the first dive to the maximum depth. No consistent diel patterns among the whales were found for any of these variables, nor were there any significant differences, except for SDUR, which differed with light level for two tags: D-1 (ANOVA, $F_{[2,30]}$ = 7.14, p = 0.003) and DZ-6 (ANOVA, $F_{[2,60]}$ = 4.30, p = 0.018).

Although day and night periods did not differ significantly for tag D-1, the geometric mean SDUR for twilight periods (12.3 min, 95% CI = 9.1–16.8 min, n = 7) was about twice as long as those for the day (5.6 min, 95% CI = 4.6–6.9 min, n = 16) or night (6.4 min, 95% CI = 4.9–8.3 min, n = 10) periods. This difference was influenced by heavy ice cover (≥90%) encountered by this whale on 29 September. Calculated values for SDUR for the two twilight periods that day (30.4 min) were extreme outliers in the distribution for this whale (Fig. 2). Excluding these two sampling periods from the analysis yielded twilight periods with slightly longer SDURs (geometric mean = 8.6 min, 95% CI = 6.3–8.0 min, n = 5) than those of the day or night periods, but not significantly so (ANOVA, $F_{[2,28]}$ = 2.33, p = 0.12).

For tag DZ-6, the SDUR was 1.5 times longer (95% CI = 1.1–2.0 times longer) for night periods (geometric mean = 11.7 min, 95% CI = 10.1–13.7 min, n = 16) than for twilight periods (geometric mean = 8.0 min, 95% CI = 6.8–9.4 min, n = 14). Daylight sampling periods had intermediate SDURs (geometric mean = 10.0 min, 95% CI = 9.0–11.1 min, n = 33) that did not differ significantly from those of either the night or twilight periods.

Mackenzie Canyon

Whales DZ-4 and DZ-2 made long deep dives and spent most of their time deeper than 48 m in Mackenzie Canyon, and whale D-2 made long dives in this region. These dives were made between 10 and 14 September.

Whale DZ-4 was located 64 times during the almost 11 d we received dive and surfacing data (see Fig. 5 in Mate et al. 2000). It moved into waters 50–200 m deep in Mackenzie Canyon on 10 September, made a short excursion back into Mackenzie Bay late on 12 September, and then returned to the deeper waters of the canyon for the last 2 d of monitoring. During three extended bouts in Mackenzie Canyon, most soundings made by DZ-4 were longer than 16 min, with the longest dives from 18 to 26 min. These bouts occured on 11, 13, and 14 September and lasted for 16, 15, and 13 h, respectively. During these three bouts, whale DZ-4 made repeated deep dives, with maximum dive depths ranging from 80 to 144 m, and spent most of its time at depths greater than 48 m: 34–78% (mean = 69 ± 15.9%, n = 6), 58–81% (mean = 66 ± 10.0%, n = 5), and 58–80% (mean = 71 ± 9.6%, n = 6).

Whale DZ-2 entered water >200 m deep in Mackenzie Canyon on 10 September (see Fig. 7 in Mate et al. 2000). Duration data were received for only 9 h while DZ-2 was in Mackenzie Canyon. Of the 22 sounding dives, 82% were >19 min long, with the longest dive each period being 30–32 min. We received dive-depth data for four sampling periods. Of 31 dives deeper than 16 m, 3 were to depths between 49 and 96 m and 22 were to depths >96 m, the deepest dives being to 112, 128, 160, and 144 m. During the last 17 h it was monitored, whale DZ-2 spent from 61 to 78% of its time (mean = 71% ± 5.6, n = 5) between 97 and 200 m deep.

Whale D-2 was located in Mackenzie Canyon waters 100–200 m deep on 12 September (see Fig. 9 in Mate et al. 2000), but data from just one sampling period were obtained. All six sounding dives were >19 min long, the longest dive being 31 min. The SDUR, 26 min, was longer than for any other period. Data received for the periods 24 h before and 24 h afterward also had high percentages of sounding dives >19 min long (67 and 71%), the longest dives being 25 and 29 min, respectively. Unfortunately, the 24-h gaps in data and the lack of locations for 11 and 13 September make it unclear if this whale engaged in extended bouts of long dives in Mackenzie Canyon like DZ-4 and DZ-2.

Discussion

The majority of dives monitored for every whale (64–92%) were short (≤1 min; Fig. 1). For whales with depth-monitoring tags, the majority of dives (68–93%) were also shallow (≤16 m; Fig. 4) and there was an extremely high correlation ($r \geq 0.95$) between the numbers of short and shallow dives. These results agree well with visual studies. Bowhead whales typically make a short dive between breaths during a surfacing sequence and then make a longer sounding dive (Carroll and Smithhisler 1980; Rugh and Cubbage 1980). Aerial observations indicate that they are often visible beneath the water and do not dive deeply during a surfacing sequence (Würsig et al. 1984; Dorsey et al. 1989). Researchers studying bowhead whale surfacing and diving behavior visually count this series of short dives as part of a "surfacing" and measure the interblow interval. The mean interblow intervals for presumably undisturbed non-calf bowhead whales in the Beaufort and Chukchi seas reported in visual studies (Table 5) range from 11.2 to 17.9 s, with an average of 3.2–12.6 blows/surfacing sequence. This translates into 69–92% of all dives being short series dives.

Though bowhead whales must surface to breathe, most of their activities take place under water. The tags we put on bowhead whales were exposed to the air for an average of 4.0–7.3% of a sampling period (Table 3), with the remaining time spent under water. Tagged bowhead whales spent little time resting at the surface. The longest surface duration recorded was 14 min, and surface intervals longer than 3.5 min were recorded in <1% of sampling periods. Ice-based observers can see some exposed body part of bowhead whales migrating past Point Barrow in spring for 3.1% (Carroll and Smithhisler 1980) to 5.2% (Zeh et al. 1993) of the time. Tags would not be exposed to the air the entire time that "some body part was visible," so it might be expected that tags would record less rather than more overall time at the surface. However, animals in the cited studies were actively migrating, whereas tagged whales were monitored during late summer, when bowhead whales are prone to remaining at the surface between blows if they are not actively traveling (Würsig et al. 1984). Bowhead whales have been reported to rest at the surface for over an hour (Carroll and Smithhisler 1980). Either tagged whales did not rest at the surface for that long or their surface resting posture did not constantly expose the tag to the air.

Comparing surfacing rates for tagged bowhead whales with data from visual studies is more problematic. Mean blow rates (blows/min), calculated from the number of blows per surfacing, the duration of surfacings, and the duration of dives, rather than surfacing rates (surfacings/h) have been published for several species of large whales. Mean blow rate describes the respiratory activity of a whale over a longer time period than do any of the constituent variables from which it is calculated (Würsig et al. 1984), but comparisons of mean blow rates between species or even between studies of the same species have been confounded by the use of two different methods of calculation (Dorsey et al. 1989). In method 1, the total number of blows during a series of surfacing-dive cycles is divided by the total duration of these cycles (Sumich 1983; Würsig et al. 1986), while in method 2, a blow rate is calculated for each surfacing–dive cycle and then a mean is computed for the number of surfacing–dive cycles observed (Würsig et al. 1984; Dolphin 1987*a*, 1987*b*).

Method 1 gives a better estimate of absolute blow rate and can be approximated by dividing the mean number of blows per surfacing by the sum of the mean durations for surfacings and dives (Dorsey et al. 1989). For comparison, we recalculated mean blow rates (blows/h) for bowhead whales in the Beaufort and Chukchi seas from 16 sets of published values reported in observational studies (Table 5). Assuming one blow for every surfacing recorded, the mean blow rate for tagged whales (Table 5) falls in the lower part of the range of values calculated from visual data. Any or all of the assumptions made in order to convert surfacing rate to blow rate for tagged whales may be violated during a given sampling period. If tags were exposed when no breath (blow) occurred, the blow rate for the period would be overestimated. If the whale took multiple breaths without submerging the tag for 6 s or breathed without exposing the tag, the blow rate for the period would be underestimated.

We did not conduct the extensive follow-up observations of tagged animals necessary to evaluate bias quantitatively, but it seems more likely that our sampling method underestimated rather than overestimated blow rates. Bowhead whales sometimes submerge for less than 6 s or do not submerge at all between blows, and they may expose only their blowholes or break ice to breathe (Carroll and Smithhisler 1980; Rugh and Cubbage 1980; Würsig et al. 1984; Carroll et al. 1987; Richardson et al. 1987; Ljungblad et al. 1988; Dorsey et al. 1989; George et al. 1989; Wartzok et al. 1990[3]; Zeh et al. 1993). Mean blow rates calculated from visual studies are likely to be biased upward because mean dive times (which make up the bulk of the time in the denominator) are biased downward, owing to the difficulty of keeping track of and identifying individual whales after long dives (Würsig et al. 1984; Dorsey et al. 1989; Richardson et al. 1995), but there is no reason to suspect that the other constituent components of the calculation are biased. Indeed, in a study of blue whales (*Balenoptera musculus*) off the California coast in which surfacing–blow rates calculated from boat-based visual observations were compared with those recorded by tags similar to ours, higher rates were found for the visual observations (Lagerquist 1997). Considering the potential biases of each sampling method, true blow rates probably lie between the blow rate values calculated for tagged whales and from observational studies. Mean surfacing rates for bowhead whales in this study (Table 3) were lower than those for either right whales (mean = 42.2 ± 14.8 surfacings/h, n = 7, range = 27.3–71.8 surfacings/h; Nieukirk 1992) or blue whales (mean = 40.8 ± 14.4 surfacings/h, n = 12, range = 16.8–63.6 surfacings/h; B.A. Lagerquist, personal communication) equipped with similar tags (ANOVA, p = 0.038).

The mean percentage of time that tagged bowhead whales were potentially visible from the air was also lower than that

[3] 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 5. Mean values for respiration and dive variables for bowhead whales in the Beaufort and Chukchi seas, from visual studies and this study of tagged whales.

	Mean interblow interval (s)							
Source	Visible	Under water	Total	Mean no. of blows/surfacing	Mean dive time (min)	Mean duration of surfacing (min)	Mean blow rate[a] (blows/h)	Percentage of time visible from the air[b]
Carroll and Smithhisler 1980	4.7 (31)	10.8 (30)	15.5	6.57 (63)	15.6 (63)	1.52	22.8	8.9
Carroll et al. 1987								
Feeding, 1980–1985			11.9 (361)	12.6 (37)	14.70 (16)	2.32 (39)	44.4	13.6
Migrating, 1980–1985			13.7 (140)	6.5 (78)	11.72 (156)	1.59 (19)	28.8	11.9
Dorsey et al. 1989								
1980			12.9 (915)	4.8 (70)	2.25 (25)	1.25 (99)	82.2	35.7
1981			13.0 (1113)	4.2 (194)	3.80 (80)	1.06 (248)	51.6	21.8
1982			14.9 (795)	7.4 (58)	12.08 (51)	2.05 (70)	31.2	14.5
1983			17.0 (866)	3.2 (299)	1.88 (140)	1.05 (204)	65.4	35.8
1984			11.6 (1472)	5.5 (75)	6.27 (37)	1.10 (94)	45.0	14.9
Ljungblad et al. 1988								
Western Beaufort			13.1 (158)	9.2 (10)	17.93 (10)	1.82 (13)	28.2	9.2
Western Aleutian			13.0 (49)	8.5 (8)	17.80 (4)	1.81 (8)	25.8	9.2
Arctic Star			15.3 (132)	3.8 (19)	14.15 (6)	1.07 (21)	15.0	7.0
Western Polaris			14.8 (246)	8.0 (24)	16.17 (4)	1.97 (25)	26.4	10.9
Rugh and Cubbage 1980	6.1 (112)	11.6 (50)	17.9 (145)	—	7.5 (3)	—	—	—
Richardson et al. 1987								
1985			12.05 (480)	6.18 (17)	7.07 (5)	1.56 (36)	43.2	18.1
1986			11.24 (816)	5.08 (51)	6.32 (23)	0.99 (78)	41.4	13.5
Wartzok et al. 1990, see footnote 3			16.5 (388)	3.6 (52)	4.0 (22)	0.9 (52)	43.8	18.4
Zeh et al. 1993	4.7 (1701)	7.4 (1531)	12.1	7.4 (184)	9.9 (41)	1.3 (184)	39.6	11.6
Unweighted mean ± SD	5.2±0.81 (3)	10.0±2.3 (3)	13.91±2.01 (17)	6.41±2.45 (16)	9.9±5.49 (17)	1.48±0.43 (16)	39.6±16.8 (16)	16.2±8.99 (16)
Unweighted mean ± SD in this study				4.5±1.1 (8)	10.4±2.4 (8)		26.4±9.0 (8)	11.1±2.4 (8)

Note: Values in parentheses are sample sizes.
[a]Calculated as 60 × [mean number of blows per surfacing/(mean duration of surfacing + mean dive time)].
[b]Calculated as 100 × [mean duration of surfacing/(mean duration of surfacing + mean dive time)].

calculated from visual studies (Table 5). Like mean blow rates, methods of calculating percentage of time that bowhead whales are visible from the air in visual studies have varied. We used the method recommended by Dorsey et al. (1989) to recalculate this percentage from observational studies. The potential methodological biases discussed for surfacing–blow rates carry over to calculations here. All the calculations assume that whales are visible from the air between serial dives during a surfacing sequence and, thus, likely yield maximum values. In the field, the depth to which whales dive and environmental conditions, such as water turbidity, sea state, cloud cover, ice cover, and light, are likely to affect the time that animals are actually visible.

Tags recorded 9573 sounding dives in our study. Individual bowhead whales tagged in this study showed highly variable SDUR values (Fig. 2). Tagged whales exhibited bouts of sounding dives of similar duration, both short and long (e.g., 20 h of predominantly short dives and 16-, 15-, and 13-h bouts of predominantly long dives for whale DZ-4). Although Würsig et al. (1984) observed that "bowheads tend to make a series of dives of similar duration rather than alternating long and short dives," the extended time over which this can occur was previously unknown. A qualitative comparison of sounding dives between our study and visual studies is possible. Mean dive times reported in these studies range from 1.88 to 17.93 min (Table 5), with a total of 686 timed "dives." We defined a sounding dive as being >1 min long. In visual studies a "dive" was judged to be a sounding dive on the basis of either (*i*) raising of the flukes or a pronounced body flexion or (*ii*) a submergence greater than some specified period of time (e.g., 75 s in Rugh and Cubbage 1980; 60 s in Würsig et al. 1984; 15 s in Dorsey et al. 1989). Mean SDUR of tagged whales (10.4 ± 2.4 min, n = 8 whales) was comparable to the mean of "dive" times from visual studies (9.9 ± 5.49 min, n = 17 studies) (Table 5).

Although only about 1% of the sounding dives reported by eight tags could have exceeded 35 min, five of the eight tags were submerged for at least 61 min in one or more sampling periods. For three whales (tags D-1, DZ-2, and DZ-4), these long submergences appear to be extreme outliers, whereas for the other two (tags DZ-1 and DZ-5), they may be viewed as part of the skewed distribution of longest dives (Fig. 3). Were these long submergences real "dives" or artifacts of the sampling method? Bowhead whales have reportedly remained submerged for over an hour. Harpooned bowhead whales have dived for 30, 40, and 60 min in the North Atlantic (Scoresby 1820) and 80 min in the North Pacific (Scammon 1874). Carroll and Smithhisler (1980) refer to an unpublished 1964 manuscript by D.C. Foote which claims that bowhead whales can dive for up to 75 min if they are injured, frightened, or otherwise greatly disturbed.[4] Some of the longest dives recorded for undisturbed bowhead whales include visual observations lasting 26.7 min (Carroll and Smithhisler 1980) and 30.98 min (Würsig et al. 1984), and time between very high frequency (VHF) radio-tag signals of 32.3 min (Wartzok et al. 1990, see footnote 3) and 41 min (Finley and Goodyear 1993[5]). However, individual whales are difficult to track and identify after long dives (Würsig et al. 1984; Dorsey et al. 1989; Richardson et al. 1995), and the number of dives sampled in these visual studies (Table 5) is an order of magnitude less than those recorded in our study. Dive duration measured as time between received high-frequency (HF)/VHF radio signals may be biased upward, since all signals may not be received during a surfacing sequence, but the bias should be relatively small compared with the dive duration (Wartzok et al. 1990, see footnote 3).

Surfacing behavior that does not expose a tag at the surface could explain some of the very long dives recorded by several animals. To breathe in areas where extensive ice cover exists, bowhead whales may expose just their blowholes in small pools of open water; they regularly break ice up to 20 cm thick and even 60 cm thick (George et al. 1989). Tags would remain under water in these circumstances, registering longer and fewer dives than actually occurred. Three tagged whales had lower surfacing rates and longer sounding dives when they were in ice cover ≥90% (Table 4). The longest dives recorded for D-1, and 92% of the sampling periods with dives ≥61 min long recorded for whale DZ-1, were in areas with ice cover ≥90%. However, not all dives ≥61 min long were made in heavy ice conditions. Tags DZ-1, DZ-2 and DZ-4 each reported one period in which the duration of longest submergence was at least 61 min while they were in open water. It is possible that resting bowhead whales exposing only their blowholes to breathe for over an hour (Carroll and Smithhisler 1980) might not expose their tag to the surface but, for whales DZ-1, DZ-2, and DZ-4, the maximum depth for the period (48, 16, and 16 m respectively) was recorded during the ≥61-min submergence. While it seems likely that some of the long "dives" were artifacts of surfacing behavior that kept tags submerged, some may have been real dives.

This is the first study of bowhead whales to include measuring dive depths, investigating the relationship between dive depth and duration, and examining where in the water column time is spent. All five whales dived to >100 m depth and whales DZ-6 and DZ-1 dived to >200 and >300 m depth, respectively (Table 2). Previous information on depths to which bowhead whales can dive has been anecdotal and indirect. In the western Arctic, bowhead whales surface with mud streaming from their mouths in water up to 40 m deep (Richardson et al. 1995). In the eastern Arctic near Isabella Bay, Baffin Island, bowhead whales feed in troughs 200 m deep, where the highest concentrations of copepods are at depths >100 m (Finley 1987[6], 1990). Although dive depth significantly influenced duration for most tagged bowhead whales, it was not a good predictor of the dive's duration

[4] D.C. Foote. 1964. Observations of the bowhead whale at Point Hope, Alaska. Geography Department, McGill University, Montréal, Que., Canada.

[5] K.J. Finley, and J.D. Goodyear. 1993. Dive patterns and feeding habitat of the bowhead whale in Baffin Bay. *In* Abstracts from the Tenth Biennial Conference of The Society for Marine Mammalogy on the Biology of Marine Mammals, held at Galveston, Tex., 11–15 November 1993. p. 48. [Abstr.]

[6] K.J. Finley. 1987. Continuing studies of the eastern stock of bowhead whale at Isabella Bay, Baffin Island, 1986. Report by LGL Ltd., Toronto, for World Wildlife Fund Canada, 60 St. Clair Avenue East, Suite 201, Toronto, ON M4T 1N5, Canada.

(Fig. 6). Theory suggests that deeper dives should be of longer duration for diving animals utilizing a resource at depth (Kramer 1988; Houston and Carbone 1992). There is ample evidence of this for many air-breathing aquatic animals, including sea turtles (Eckert et al. 1986), diving birds (Stonehouse 1967; Kooyman et al. 1992; Williams et al. 1992), pinnipeds (Gentry et al. 1986; Kooyman and Gentry 1986; Feldkamp et al. 1989), odontocetes (Martin and Smith 1992; Martin et al. 1994), and mysticetes (Dolphin 1987*a*; Lagerquist 1997). Factors other than maximum depth may also strongly influence dive duration. Individual variation, prey depth and abundance, and the activity in which animals engage are factors likely to affect dive time.

Three whales (DZ-2, DZ-4, and D-2) made long dives in the vicinity of Mackenzie Canyon between 10 and 14 September. At least two of these whales were making extended bouts of deep dives in which they spent most of their time at depths ≥48 m. We suspect that these animals were feeding in the water column or near the bottom on dense zooplankton patches, probably calanoid copepods. Feeding on zooplankton, primarily copepods and euphausiids (Lowry 1993), is the predominant activity for bowhead whales that summer in the Beaufort Sea (Würsig et al. 1985). Baleen whales must feed where zooplankton is concentrated (Brodie et al. 1978). Zooplankton distribution in the Beaufort Sea is patchy both vertically and horizontally. Patches are usually 5–10 m thick and often extend several kilometres in the horizontal plane, with the thickest layer typically found either midwater or near the bottom (Griffiths et al. 1987). Bowhead whales seem to be able to find and exploit these patches. Zooplankton samples collected near feeding bowhead whales yielded higher prey biomass than samples taken elsewhere in the region (Griffiths and Buchanan 1982; Bradstreet and Fissel 1986; Bradstreet et al. 1987; Griffiths et al. 1987; Wartzok et al. 1990, see footnote 3). Mackenzie Canyon is a productive area in which zooplankton is at times concentrated (Thomson et al. 1986). In late summer, *Calanus hyperboreus* and *Calanus glacialis*, two important copepod prey species for bowhead whales in the Beaufort Sea (Lowry and Burns 1980; Lowry and Frost 1984; Lowry 1993), make a seasonal ontogenetic vertical migration to deeper water (>50 m) to overwinter, although when and to what depths they descend may vary with species, life stage, and geographic location (Maclellan 1967; Prygunkova 1968; Dawson 1978; Geinrikh et al. 1983; Kosobokova 1982; Longhurst et al. 1984; Conover 1988; Hirche 1991). *Calanus hyperboreus* and *C. glacialis* that have descended to deeper water in summer have substantially greater lipid content than those found in the upper 50 m (Head and Harris 1985; Kosobokova 1990) and would be a high-calorie food source for bowhead whales. We recommend that future studies to determine the importance of bowhead whale feeding areas examine zooplankton distribution and abundance to depths of at least 200 m.

When three whales were in heavy ice conditions, their tags recorded fewer and longer dives and more time exposed to the air during fewer surfacings (Table 4). However, calculations suggest that these animals would have been visible from the air for less time (Table 4). Whale DZ-1 also made more dives >48 m deep and spent more time at depths >32 m (Figs. 7B and 7C). These data suggest the whales' strategy for dealing with areas of heavy ice: long dives to the deeper portion of the water column to avoid deep-keeled ice and longer surface times when open water is found. The four 1-h periods where tag DZ-1 did not break the surface coupled with the 23 very long "dives" (≥61 min) recorded in heavy ice conditions suggest that this animal may have regularly broken ice to breathe.

Most of these findings are consistent with observed behavior of bowhead whales in ice. Würsig et al. (1984) noted longer dive times and more blows per surfacing for whales in ice than for those in open water and that about 75% of the animals observed in ice rested quietly when at the surface. Richardson et al. (1995) reported significantly shorter dive times for bowhead whales migrating through areas with 65–90% ice cover in the fall of 1983 (5.5 min) than for whales migrating through areas with <10% ice cover in the fall of 1985 and 1986 (18.2 min), but noted that the 1983 dive times were probably biased downward by the difficulty of resighting animals in heavy ice conditions after a long dive. Although the number of short series dives in a surfacing sequence decreased slightly, the increased percentage of surface time and the longer duration of longest surface times (at least for two animals) in heavy ice suggest that the whales may have rested at the surface between blows. Thus, the number of blows per surfacing sequence may have increased without a corresponding increase in short-series dives being recorded by the tag.

The directed westward movement of whale DZ-1 during the time it was in heavy ice (Mate et al. 2000) suggests that migration was its dominant activity. Perhaps the most interesting aspect of this whale's behavior during this interval was that it spent much less time near the surface (Fig. 7C). Although submerged swimming offers hydrodynamic advantages over swimming at the surface, animals need only submerge to about three times their body diameter to avoid surface-drag effects (Hertel 1966, p. 227). Bowheads would not have to exceed depths of our shallowest bin (16 m) for hydrodynamic considerations. However, the deep keels of ice floes can reach to 50 m below the surface (LaBelle et al. 1983). Bowhead whales migrating under a frozen lead where the water was 30 m deep avoided an area of deep-keeled multiyear ice and left bottom sediments in and around the hummocks created where they broke newly formed ice 14–18 cm thick to breath (George et al. 1989). Ellison et al. (1987) suggest that bowhead whales may use the differential surface reverberations of their calls (at distances of 1–2 km) to discriminate between areas of rough-bottomed deep-keeled multiyear ice and open water or smooth-bottomed young ice thin enough to break through to breathe. These authors modeled ice keels 10 m deep and a whale producing sound at 15 m, but they noted that the path of propagation of sound might allow bowhead whales in deep Arctic waters to "acoustically image" beyond immediate obstructions if sounds were broadcast below the horizontal. Bowhead whales may travel and vocalize at greater depths, to image ice conditions acoustically at greater distances and move more efficiently through or around areas with deep-keeled multiyear ice.

This is the first study to monitor dive and surfacing characteristics of individual bowhead whales day and night for up to 33 days. The general lack of diel patterns recorded for tagged bowhead whales suggests that they continue their behavior regardless of light level. For many air-breathing nektonic species, diel changes in diving behavior are linked to diel vertical migration of their prey. In 1988, right whales (*Eubalaena glacialis*) in the Great South Channel made longer dives during the day when copepods migrated to near the bottom and shorter dives at night when copepods were near the surface but, in 1989, when copepods did not vertically migrate, no such difference in dive duration was found (Winn et al. 1995). Other examples include sea turtles (Eckert et al. 1989), penguins (Kooyman et al. 1992; Williams et al. 1992), and pinnipeds (Croxall et al. 1985; Feldkamp et al. 1989). With diel vertical migration absent or weak for most species, vertical distribution of the bowhead whale's zooplankton prey in Arctic waters is tied more to season than to time of day (Bogorov 1946; Kosobokova 1978; Longhurst et al. 1984; Sameoto 1984). Even the two tagged whales that made long deep dives in Mackenzie Canyon did so during day, twilight, and night. Migration also seemed to continue around the clock for whale DZ-1. No discernible time of day was favored for rest.

Studying diving behavior using satellite telemetry requires a thoughtful strategy. From the standpoint of data returns, transmitting information whenever possible throughout the day (DZ tags) rather than for limited periods (D tags) was clearly the superior method. DZ tags returned from 53 to 89% of the possible sampling periods, whereas the two D tags returned only 23 and 37% (Table 1). Tags were positioned well on all eight whales, so the likelihood of a tag being exposed during a surfacing was equal for all whales. Thus the difference reflects transmission schedules. If no transmissions were received during the 100 min that D tags were scheduled to transmit, four sampling periods of data (12 h) were lost. DZ tags, on the other hand, transmitted data for each sampling period during the next two sampling periods (usually 6 h). Unlike archival time–depth recorders (TDRs) that store data and must be retrieved, data recovery from Argos-monitored radio tags is limited to 256-bit transmissions while satellites are overhead. Archival TDRs are suitable only for animals that can be reliably recaptured, such as turtles, birds, and pinnipeds, or for short-term deployment on cetaceans staying in one area (e.g., Croll et al. 1998). Depending on the objectives of the study, one can choose to transmit either compressed summary data for a larger number of dives and surfacings, as we did, or detailed time–depth data at a finer scale for a smaller subset of dives (e.g., Martin and Smith 1992; Martin et al. 1994). Though fine-scale details of individual dives are lost, summary data from satellite-linked tags provide an accurate representation of actual diving behavior that is qualitatively similar to that recorded simultaneously by TDRs, if consideration is given to how tags are programmed (Burns and Castillini 1998).

This study demonstrates the utility of microprocessor-controlled data loggers linked with satellite radiotelemetry for gathering dive and surfacing data on large whales. These methods allow data to be gathered around the clock from several animals simultaneously over a wide geographic range in any weather. Dive data linked to location information provide unique insight into habitat utilization. The first direct measurements of dive depths and time at depth gathered here suggest that assessments of feeding areas must examine potential prey availability to at least 200 m depth. The number of dives and surfacings sampled from these eight whales is an order of magnitude greater than in all previous visual studies of bowhead whales combined, and provides a wealth of information on the variability displayed by individual whales as well as on variability among animals. Understanding this natural variability may ultimately allow us to better measure the effects of human activities on such endangered species.

Acknowledgements

This research was authorized under the Marine Mammal Protection Act and Endangered Species Act (National Marine Fisheries Service (NMFS) permit No. 492) and by the Canadian Department of Fisheries and Oceans (permit F-91/92-03). We thank Bill Koplin, owner and captain of the R/V *Annika Marie*, for his skill, humor, and preparation; Bill Koplin and Toby Martin for help in the field; Rod Mesecar, Toby Martin, and Sharon Nieukirk for assistance in tag development and construction; Tomas Follett for development of location data editing software; the Canadian Coast Guard for ice-analysis charts; Gary Hufford for satellite images and interpretation of sea ice; Vicki Hoover for support, encouragement, and help in assembling an early version of the manuscript; Veryl Barry for help and coordination in the office; Sallie Beavers, Sharon Nieukirk, Vicki Hoover, Martha Winsor, and two anonymous reviewers for editorial input that improved the manuscript; U.S. Minerals Management Service (MMS) and the Canadian Department of Indian and Northern Affairs for funding; and our MMS technical representatives: Cleve Cowles, Warren Horowitz, Jerome Montague, Judy Wilson, and especially Jerry Imm. We are grateful for equipment donations from Zenith, Memorex, Toshiba, Gates, Fred Biller, Crescent Manufacturing, and the employees of Hewlett-Packard in Corvallis, Oreg. This research was partially funded by generous private and corporate donations to the Oregon State University Endowed Marine Mammal Research Program.

References

Bogorov, B.G. 1946. Peculiarities of diurnal vertical migrations of zooplankton in polar seas. J. Mar. Res. **6**: 25–32.

Bradstreet, M.S.W., and Fissel, D.B. 1986. Zooplankton of a bowhead whale feeding area off the Yukon Coast in August 1985. Report by LGL Ltd., Toronto, to the Canadian Department of Indian Affairs and Northern Development, Ottawa, Ont.

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

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.

Burns, J.M., and Castellini, M.A. 1998. Dive data from satellite tags and time–depth recorders: a comparison in Weddell seal pups. Mar. Mamm. Sci. **14**: 750–764.

Carroll, G.M., and Smithhisler, J.R. 1980. Observation of bowhead whales during spring migration. Mar. Fish. Rev. **42**: 80–85.

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

Conover, R.J. 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. Hydrobiologia, **167/168**: 127–142.

Croll, D.A., Tershey, B.R., Hewitt, R.P., Demer, D.A., Fiedler, P.C., Smith, S.E., Armstrong, W., Popp, J.M., Kiekhefer, T., Lopez, V.R., Urban, J., and Gendron, D. 1998. An integrated approach to the foraging ecology of marine birds and mammals. Deep-Sea Res. Part II. Top. Stud. Oceanogr. **45**: 1353–1371.

Croxall, J.P., Everson, I., Kooyman, G.L., Ricketts, C., and Davis, R.W. 1985. Fur seal diving behavior in relation to vertical distribution of krill. J. Anim. Ecol. **54**: 1–8.

Davis, R.A., Koski, W.R., Richardson, W.J., Evans, C.R., and Alliston, W.G. 1982. Distribution, numbers and productivity of the Western Arctic stock of bowhead whales in the eastern Beaufort Sea and Amundson Gulf, summer 1981. Report by LGL Ltd., Toronto, for Sohio Alaska Petroleum Co., Anchorage, and Dome Petroleum Ltd., Calgary. Available from The University of Calgary Library (Arctic Institute of North America Collection), Calgary, AB T2N 1N4, Canada.

Davis, R.W., Worthy, G.A.J., Würsig, B., and Lynn, S.K. 1996. Diving behavior and at-sea movements of an Atlantic spotted dolphin in the Gulf of Mexico. Mar. Mamm. Sci. **12**: 569–581.

Dawson, J.K. 1978. Vertical distribution of *Calanus hyperboreus* in the central Arctic Ocean. Limnol. Oceanogr. **23**: 950–957.

Dolphin, W.F. 1987*a*. Ventilation and dive patterns of humpback whales, *Megaptera noveaeangliae*, on their Alaskan feeding grounds. Can. J. Zool. **65**: 83–90.

Dolphin, W.F. 1987*b*. Dive behavior and estimated energy expenditure of foraging humpback whales in southeast Alaska. Can. J. Zool. **65**: 354–362.

Dorsey, E.M., Richardson, W.J., and Würsig, B. 1989. Factors affecting surfacing, respiration, and dive behaviour of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea. Can. J. Zool. **67**: 1801–1815.

Eckert, S.A., Nellis, D.W., Eckert, K.L., and Kooyman, G.L. 1986. Diving patterns of two leatherback sea turtles (*Dermochelys coriacea*) during internesting intervals at Sandy Point, St. Croix, U.S. Virgin Islands. Herpetologica, **42**: 381–388.

Eckert, S.A., Eckert, K.L., Ponganis, P., and Kooyman, G.L. 1989. Diving and foraging behavior of leatherback sea turtles (*Dermochelys coriacea*). Can. J. Zool. **67**: 2834–2840.

Ellison, W.T., Clark, C.W., and Bishop, G.C. 1987. Potential use of surface reverberation by bowhead whales, *Balaena mysticetus*, in under-ice navigation: preliminary considerations. Rep. Int. Whaling Comm. **37**: 329–332.

Feldkamp, S.D., DeLong, R.L., and Antonelis, G.A. 1989. Diving patterns of California sea lions, *Zalophus californianus*. Can. J. Zool. **67**: 872–883.

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**: 137–152.

Geinrikh, A.K., Kosobokova, K.N., and Rudyakov, Yu.A. 1983. Seasonal variations in the vertical distribution of some prolific copepods of the Arctic basin. Can. Transl. Fish. Aquat. Sci. No. 4925. [Translated from Biologia Tsentral'nogo Arkticheskogo Basseina, 1980, pp. 155–166.]

Gentry, R.L., Kooyman, G.L., and Goebel, M.E. 1986. Feeding and diving behavior of northern fur seals. *In* Fur seals, maternal strategies on land and at sea. *Edited by* R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 61–78.

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.

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, for 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 hydroaccoustics. *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. 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.

Head, E.J.H., and Harris, L.R. 1985. Physiological and biochemical changes in *Calanus hyberboreus* from Jones Sound, NWT during the transition from summer feeding to overwintering condition. Polar Biol. **4**: 99–106.

Heide-Jørgensen, M.P., and Dietz, R. 1995. Some characteristics of narwhal, *Monodon monoceros*, diving behaviour in Baffin Bay. Can. J. Zool. **73**: 2120–2132.

Hertel, H. 1966. Structure–form–movement. Reinhold Publishing Corp., New York.

Hiby, A.R., and Hammond, P.S. 1989. Survey techniques for estimating the abundance of cetaceans. Rep. Int. Whaling Comm. Spec. Issue No. 11. pp. 47–80.

Hirche, H.-J. 1991. Distribution of dominant calanoid copepod species in the Greenland Sea during late fall. Polar Biol. **11**: 351–362.

Houston, A.I., and Carbone, C. 1992. The optimal allocation of time during the diving cycle. Behav. Ecol. **3**: 255–265.

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.

Kooyman, G.L., and Gentry, R.L. 1986. Diving behavior of South African fur seals. *In* Fur seals, maternal strategies on land and at sea. *Edited by* R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 142–152.

Kooyman, G.L., Cherel, Y., Le Maho, Y., Croxall, J.P., Thorson, P.H., Ridoux, V., and Kooyman, C.A. 1992. Diving behavior and energetics during foraging cycles in king penguins. Ecol. Monogr. **62**: 143–163.

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.

Kosobokova, K.N. 1978. Diurnal vertical distribution of *Calanus hyperboreus* Krøyer and *Calanus glacialis* Jaschnov in the Central Polar Basin. Oceanology, **18**: 476–480.

Kosobokova, K.N. 1982. Composition and distribution of the biomass of zooplankton in the central Arctic basin. Oceanology, **22**: 744–750.

Kosobokova, K.N. 1990. Age-related and seasonal changes in the biochemical makeup of the copepod *Calanus glacialis* as related to the characteristics of its life cycle in the White Sea. Oceanology, **30**: 103–109.

Kramer, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. Can. J. Zool. **66**: 89–94.

LaBelle, J.C., Wise, J.L., Voelker, R.P., Schulze, R.H., and Wohl, G.M. 1983. Alaska ice atlas. Arctic Environmental Information and Data Center, University of Alaska, 707 A Street, Anchorage, AK 99501, U.S.A.

Lagerquist, B.A. 1997. Dive characteristics of northeast Pacific blue whales (*Balaenoptera musculus*) monitored by satellite telemetry. M.S. thesis, Oregon State University, Corvallis.

Lin, S. 1970. An introduction to error-correcting codes. Prentice Hall, Englewood Cliffs, N.J.

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.

Longhurst, A., Sameoto, D., and Herman, A. 1984. Vertical distribution of Arctic zooplankton in summer: eastern Canadian archipelago. J. Plankton Res. **6**: 137–168.

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 Burns, J.J. 1980. Foods utilized by bowhead whales near Barter Island, Alaska, autumn 1979. Mar. Fish. Rev. **42**: 88–91.

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.

Maclellan, D.C. 1967. The annual cycle of certain calanoid species in west Greenland. Can. J. Zool. **45**: 101–115.

Martin, A.R., and Smith, T.G. 1992. Deep diving in wild, free-ranging beluga whales, *Delphinapterus leucas*. Can. J. Fish. Aquat. Sci. **49**: 462–466.

Martin, A.R., Kingsley, M.C.S., and Ramsay, M.A. 1994. Diving behaviour of narwhals (*Monodon monoceros*) on their summer grounds. Can. J. Zool. **72**: 118–125.

Mate, B.R., Stafford, K.M., Nawojchik, R., and Dunn, J.L. 1994. Movements and dive behavior of a satellite-monitored Atlantic whitesided dolphin (*Lagenorhynchus acutus*) in the Gulf of Maine. Mar. Mamm. Sci. **10**: 116–121.

Mate, B.R., Rossbach, K.A., Nieukirk, S.L., Wells, R.S., Irvine, A.B., Scott, M.D., and Read, A.J. 1995. Satellite-monitored movements and dive behavior of a bottlenose dolphin (*Tursiops truncatus*) in Tampa Bay, Florida. Mar. Mamm. Sci. **11**: 452–463.

Mate, B.R., Krutzikowsky, G.K., and Winsor, M. 2000. Satellite-monitored movements of radio-tagged bowhead whales in the Beaufort and Chukchi seas during the late-summer feeding season and fall migration. Can. J. Zool. **78**: 1168–1181.

Montague, J.J. 1993. Introduction. *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. 1–21.

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.

Nieukirk, S.L. 1992. Satellite monitored dive characteristics of the northern right whale (*Eubalaena glacialis*). M.S. thesis, Oregon State University, Corvallis, Oreg.

Prygunkova, R.V. 1968. On the growth cycle of *Calanus glacialis* Jaschnov in the White Sea. Dokl. Biol. Sci. **182**: 1447–1450 [Translated from Dokl. Akad. Nauk SSSR, **182**: 1447–1450.]

Ramsey, F.L., and Schafer, D.W. 1996. The statistical sleuth. Duxbury Press, Pacific Grove, Calif.

Richardson, W.J., Fraker, M.A., Würsig, B., and Wells, R.S. 1985. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: reactions to industrial activities. Biol. Conserv. **32**: 195–230.

Richardson, W.J., Würsig, B., and Greene, C.R., Jr. 1986. Reactions of bowhead whales, *Balaena mysticetus*, to seismic exploration in the Canadian Beaufort Sea. J. Acoust. Soc. Am. **79**: 1117–1128.

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.

Richardson, W.J., Finley, K.J., Miller, G.W., Davis, R.A., and Koski, W.R. 1995. Feeding, social and migration behavior of bowhead whales, *Balaena mysticetus*, in Baffin Bay vs. the Beaufort Sea—regions with different amounts of human activity. Mar. Mamm. Sci. **11**: 1–45.

Rugh, D.J., and Cubbage, J.C. 1980. Migration of bowhead whales past Cape Lisburne, Alaska. Mar. Fish. Rev. **42**: 46–51.

Sameoto, D.D. 1984. Vertical distribution of zooplankton biomass and species in northeastern Baffin Bay related to temperature and salinity. Polar Biol. **2**: 213–224.

Scammon, C.M. 1874. The marine mammals of the northwestern coast of North America together with an account of the American whale fishery. J.H. Carmany, San Francisco. (Reprinted (paperback) 1968, Dover Publications Inc., New York.)

Scoresby, W., Jr. 1820. An account of the Arctic regions, with a history and description of the northern whale-fishery. Archibald Constable, Edinburgh, Scotland. [Reprinted by David and Charles, Newton Abbot, England.]

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.

Stonehouse, B. 1967. Feeding behaviour and diving rhythms of some New Zealand shags, *Phalacrocoracidae*. Ibis, **109**: 600–605.

Sumich, J.L. 1983. Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus*. Can. J. Zool. **61**: 647–652.

Thomson, D.H. 1987. Energetics of bowheads. *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. 417–448.

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.

U.S. Department of Commerce. 1991. Tide tables 1992: high and low water predictions, west coast of North and South America, including the Hawaiian islands. U.S. Department of Commerce, Rockville, Md.

Wakerly, J. 1978. Error detecting codes, self-checking circuits and applications. North-Holland, New York.

Williams, T.D., Kato, A., Croxall, J.P., Naito, Y., Briggs, D.R., Rodwell, S., and Barton, T.R. 1992. Diving pattern and performance in nonbreeding gentoo penguins (*Pygoscelis papua*) during winter. Auk, **109**: 223–234.

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.

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.

Würsig, B., Wells, R.S., and Croll, D.A. 1986. Behavior of gray whales summering near St. Lawrence Island, Bering Sea. Can. J. Zool. **64**: 611–621.

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.