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Dive Behaviour of Belugas (*Delphinapterus leucas*) in the Shallow Waters of Western Hudson Bay

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ABSTRACT. Beluga diving was studied in western Hudson Bay, where the preferred habitat of this whale in summer is shallow coastal waters. No relationship was found between the duration of a dive and the surface interval either preceding or following it. During rare periods of intense diving, 77% of an average dive cycle was spent below the water surface. Only in waters deeper than 25 m did any whale spend more than half its time below the surface zone; in rivers, less than 15% of the time was spent at depths of 4 m or more. The frequency of long dives increased with water depth. Maximum dive duration was 15.6 min. Dives to depths of 25 m or less were of variable duration and time-depth profile; most dives exceeding 50 m had a square profile and reached the seabed. The easterly migration in early September took the whales into water deeper than 100 m for the first time in several months, and they dived frequently to the bottom during this period. No clear difference in dive capability was found between western Hudson Bay belugas and those that inhabit deeper waters farther north. The preference of this population for shallow water in summer is not dictated by an inability to dive to greater depths; belugas can utilize benthic resources throughout Hudson Bay.

Key words: beluga, white whale, Hudson Bay, diving, dive behaviour

RÉSUMÉ. On a étudié le bélouga en plongée dans l'ouest de la baie d'Hudson, où les eaux littorales peu profondes constituent l'habitat estival préféré de cette baleine. On n'a trouvé aucun lien entre la durée de la plongée et l'intervalle passé en surface qui la précède ou la suit. Durant les rares périodes de plongée intense, 77 p. cent d'un cycle moyen de plongée se déroulait sous la surface de l'eau. C'est seulement dans les eaux dont la profondeur était supérieure à 25 m que les baleines passaient plus de la moitié du temps sous la zone en surface; dans les cours d'eau, moins de 15 p. cent du temps se passait à des profondeurs de 4 m ou plus. La fréquence des longues plongées augmentait avec la profondeur de l'eau. La durée maximale de la plongée était de 15,6 mn. Les plongées à des profondeurs de moins de 25 m avaient une durée et un profil durée-profondeur variables; la plupart des plongées dépassant les 50 m avaient un profil carré et atteignaient le fond marin. Au début septembre, la migration vers l'est amenait les baleines dans des eaux dont la profondeur excédait 100 m pour la première fois depuis plusieurs mois et, durant cette période, elles plongeaient souvent en atteignant le fond. On n'a pas trouvé de différence nette dans la capacité à plonger entre les bélougas de l'ouest de la baie d'Hudson et ceux qui habitent les eaux plus profondes plus au nord. Ce n'est pas une incapacité à plonger à de plus grandes profondeurs qui dicte la préférence estivale de cette population de bélougas pour l'eau peu profonde; ils peuvent utiliser les ressources benthiques dans l'ensemble de la baie d'Hudson.

Mots clés: bélouga, baleine blanche, baie d'Hudson, plongée, comportement en plongée

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INTRODUCTION

The beluga *Delphinapterus leucas* has a northern circumpolar distribution, and most of the ca. 30 stocks currently recognized migrate between summer and winter grounds (International Whaling Commission, 2000). Diving behaviour has been relatively well studied in only one such population: that which summers in the eastern Canadian High Arctic, an area of deep channels between large islands (Martin and Smith, 1992, 1999; Martin et al., 1993, 1998). Here, the species routinely makes deep (> 300 m) and long (> 12 min) submergences, which give it competitive advantage over sympatric pinnipeds (Martin and Smith, 1999). In this area, belugas spend substantial periods of time on or near the seabed in water hundreds of metres deep, and they almost certainly feed there. They apparently seek out the deepest areas (Smith and Martin, 1994; Martin and Smith, 1999), and the species is clearly capable of making a living in deep shelf waters.

A different population of belugas summers in western Hudson Bay, some 1500 km to the south of this region. These whales are smaller (Stewart, 1994) and are commonly seen both along the coast and in the lower reaches of rivers that empty into the Bay (Fig. 1). In contrast to the

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TABLE 1. Deployment details for belugas fitted with satellite-linked data loggers and tracked in western Hudson Bay during the summer and early autumn of 1993.

Whale No.	Sex	Length (m)	Description	Capture date	Release time (local)	Tag longevity (days)
5800_93	M	3.73	White adult	July 29	17.30	56.4
5801_93	F	3.40	Light grey, with yearling calf	July 29	18.10	47.9
5803_93	F	3.25	Light grey, with calf	July 30	17.40	31.4
5805_93	M	4.11	White adult	July 29	16.13	44.6

belugas farther north, these whales spend the entire summer in very shallow water (P. Hall, A.R. Martin, P.R. Richard, unpubl. data). From their arrival at ice breakup in June until their departure towards the east in early September, these animals spend most of their time in water less than 25 m deep, and much of it in freshwater.

The current study examines diving in four belugas from this population during the summer period and the beginning of their autumnal eastward movement. Behaviour is investigated on several scales: the individual dive, the dive sequence, the day, and the season. Of particular interest is how belugas manage their time in an area where, in contrast to the population to the north, they can exploit the entire water column with ease.

MATERIALS AND METHODS

In July 1993, four adult belugas were captured individually in the lower reaches of the Churchill River, Manitoba (58˚45′N, 94˚10′W), fitted with satellite-linked data loggers on their dorsal ridge in shallow water nearby (see Martin et al., 1993 for attachment details), and released immediately. Details of the whales (two males, two females) and transmitter longevity are given in Table 1. The loggers (designed and constructed by the Sea Mammal Research Unit, UK) collected, processed, and stored dive information, then sent it to the laboratory via System ARGOS (Fancy et al., 1988). To estimate depth, the loggers measured ambient pressure every 4 s. To detect a surfacing immediately, they interrogated an optical wet/dry sensor every 0.2 s when within 5 m of the water surface. Each transmission contained 256 bits of data, which included error-checking code to facilitate the later rejection of faulty data strings.

Data were transmitted in three formats that gave different levels of resolution, and each transmission provided a "page" of information. Those of highest resolution, termed time-depth record (TDR) pages, gave 28 consecutive depth readings (accuracy ± 1 m) at 40 s intervals, covering a period of 18.7 min in one transmission. TDR pages showed the time-depth profile of dives and allowed an independent means of checking the validity of summary data (dive duration and maximum depth) contained in the other pages. Measurement intervals of 40 s are sufficiently short to detect all submergences to 20 m or more, and very few to 10 m or more are missed, but TDR pages certainly missed some short and very shallow dives. Similarly, the profiles of dives with duration several times the sampling interval are accurately portrayed, but accuracy decreases for dives of less than, say, 3 min. This type of data was therefore not used to investigate short submergences. For the four whales together, we collected a total of 113.4 hr of error-free TDR data, covering at least 1239 submergences to a minimum depth of 4 m or more.

A page of intermediate-level data provided the duration and maximum depth of nine consecutive dives, the duration of the surface interval preceding each dive (PSI), and the date and time at which the dives occurred. Since the PSI for dive *n* is also the following surface interval (FSI) for dive *n*-1, such pages were termed 'sequence' (SEQ) pages. The length of time covered by a page of this type of transmission varied from less than 30 min to more than 16 hr, depending mostly on the duration of surface intervals. A 'dive' is defined in this context, and throughout this paper, as a submergence to at least 4 m for at least 4 s. A 'surface interval' is the period between two dives, during which time the whale, by definition, did not exceed a depth of 3.9 m for more than 3.9 s. The term 'near the surface' refers to the upper 4 m of the water column, and the term 'below the surface' to the remainder of the water column.

The third (lowest resolution) format, termed 'histogram' (HIST) data, summarized dive activity during known 2 hr periods. Each page included the maximum depth reached during the period (± 4 m), the number of dives made, and three histograms: dive maximum depth, dive duration, and the proportion of time spent in particular depth bands. The threshold values between consecutive histogram bins are given in Table 2.

Data in all three formats were stored for 36 hr after collection and transmitted many times during that period to increase the probability that they would be safely received. This procedure also reduced potential bias in the data sample, which might otherwise disproportionately represent shallow-water behaviour because of a higher rate of surfacing. Data strings were later error-checked and chronologically ordered to allow the concatenation of sequential information.

To increase tag longevity, data collection and transmission functions were switched to a cycle of 24 hr off/12 hr on commencing on the seventh day after release. This schedule provided an unbiased diurnal coverage, but resulted in a discontinuous record of dive behaviour. The periods of time for which error-free TDR, SEQ, and HIST data were available for analysis are given in Table 3.

The depth of water in which a whale was swimming at a particular time was estimated from detailed bathymetric charts, using timed, satellite-derived locations for the whale.

TABLE 2. Threshold values between consecutive histogram bins used to characterize dive behaviour in known 2 hr periods.

Dive duration (min)	Depth bands (m)	Dive maximum depth (m)
0 – 4.9	0 – 3.9	< 50.9
5 – 9.9	4.0 – 8.9	51.0 – 99.9
10 – 14.9	9.0 – 25.9	100.0 – 199.9
15 – 19.9	26.0 – 50.9	
≥ 20	51.0 – 99.9	
	100.0 – 199.9	

TABLE 3. Periods of time for which error-free TDR, SEQ, and HIST data were available for analysis.

Whale No.	TDR data (hr)	SEQuence data (hr)	HISTogram data
5800_93	30.6	85.0	11.9 days, 1298 dives
5801_93	25.9	97.9	9.8 days, 946 dives
5803_93	29.1	37.7	9.4 days, 1592 dives
5805_93	27.8	96.0	10.8 days, 1140 dives

The accuracy of such estimation was dependent on two factors: the temporal proximity of a high-quality position fix and the uniformity of water depth in that region. However, on almost every occasion when an accurate depth measurement was possible, it was found that the whale had dived to the seabed at least once within an hour of the 'fix,' so maximum dive depth in a 2 hr HIST period was usually a good approximation of the maximum water depth encountered by the whale during that period. Horizontal displacement over a 2 hr period, assuming a maximum travel speed of 1.4 ms^{-1} (Smith and Martin, 1994), is unlikely to exceed 10 km and will usually be much less than this. Figure 1 shows the geographical origin of the dive data used in this analysis in relation to the local bathymetry.

To avoid possible behavioural changes due to capture and handling, data collected during the first 24 hr after release were ignored.

RESULTS

Individual Dive

The plot of dive duration on maximum depth for all whales combined (Fig. 2) demonstrates that dives to 100 m or more demanded a submergence of at least 6.7 min, but that the longest periods of breath-hold accurately measured in this study (all by male 5805_93) were achieved in dives reaching only 20 m or so. The three submergences of around 15 min in duration (maximum 15.6 min) all reached a depth of 22 m close to shore and probably reached the seabed. Unfortunately, we have no information to indicate whether these dives were active or whether, for example, the animal was simply resting, or even sleeping.

No relationship was found between the duration of a dive and the duration of the surface interval either preceding or following it (linear regression of dive duration on PSI: $r^2 = 0.2\%$, $p > 0.1$; that of FSI on dive duration: $r^2 < 0.5\%$, $p > 0.1$, even when the longest FSIs are successively eliminated to remove the effect of prolonged resting periods). The ratio of PSI to dive duration is extremely variable (Fig. 3) and reflects the fact that most dives were not made during periods of intense dive activity. Nevertheless, a cluster of points in the PSI range 2–3 min is apparent for dive durations of about 3 min or above. A more revealing picture is presented if attention is focused on periods of concentrated diving, when the whales may be approaching their physiological limit. Figure 4 shows the frequency distribution of the ratio FSI:dive duration for consecutive dives of 5 min or more (n = 108). A distinct mode of 0.2–0.4 is evident here, and the distribution has a median value of 0.3, i.e., the surface interval following a dive is 0.3 times the dive duration. Put another way, the whale spends 77% of an average dive cycle (dive duration + FSI) below the surface during sustained periods of long submersions.

For reasons discussed above, the 40 s interval between TDR measurements precludes detailed analysis of the profile of very shallow dives. What we can deduce from the three levels of data combined is that dives not exceeding 25 m depth are of variable duration and profile. Two typical shallow-water behaviours are illustrated in Figure 5, both from female 5801_93. Figure 5a shows a mixed sequence of six short consecutive dives to around 20 m, some with apparent 'U-shaped' profiles, others with interruptions on the descent or ascent. In contrast, the four dives illustrated in Figure 5b are uniformly 'square-shaped' and to exactly the same depth (13 m). The third of these dives shows the whale spending about 280 s on the seabed before swimming to the surface for a respiratory interval of rather more than 40 s, then returning to the seabed. Figure 5c shows a similar-looking series of dives, but these were carried out (by male 5805_93) in deep water (100 m) and were part of a sequence of long (> 5 min) submergences. Such mid-water dives were not usual (they comprise 28% of 67 submergences lasting at least 3 min in water at least 50 m deep).

Because of the coastal habitat of this beluga population and the bathymetry of western Hudson Bay, the study animals spent little time in deep water; consequently, only a small proportion of the recorded submergences exceeded 25 m in depth. Most of these were recorded towards the end of the study, as the whales were starting to move eastward. TDR data revealed the profile of 17 dives that reached depths exceeding 50 m. Of the 17, only 8 dives exceeded 100 m, and 7 of those 8 were made by male 5800_93 during easterly autumnal migration. The time-depth profile of all the 100+ m dives was "square-shaped": a steady, uninterrupted descent was followed by a period at a constant depth and completed by a uniform ascent. Six of the nine 50–100 m dives were also of this shape. Another was similar but had a slow start to the ascent, and the remaining two were V-shaped, i.e., the ascent immediately followed the descent (Martin et al., 1998).

Vertical speeds were calculated for dives that exceeded 85 m maximum depth, allowing the measurement of even

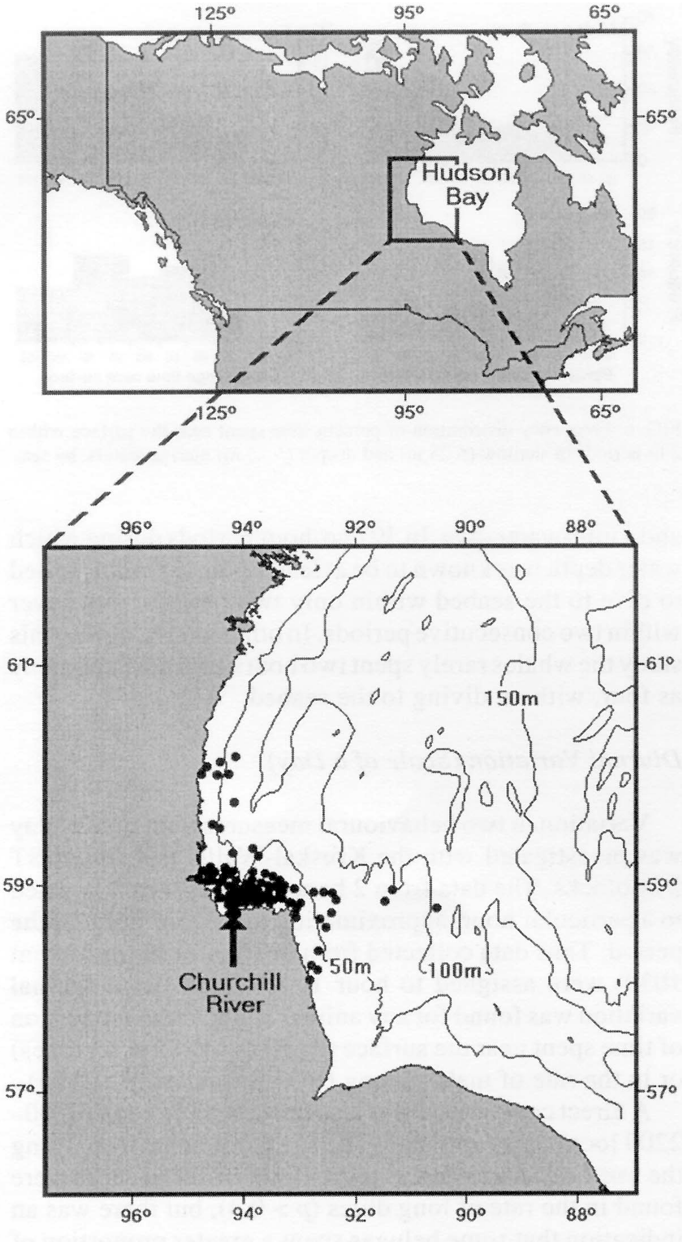

FIG. 1. Study area map. All whales were tagged near the mouth of the Churchill River. The average location of a tagged whale every 6 hours is shown by a dot (●), so the geographical distribution of dots approximately represents the distribution of dive data.

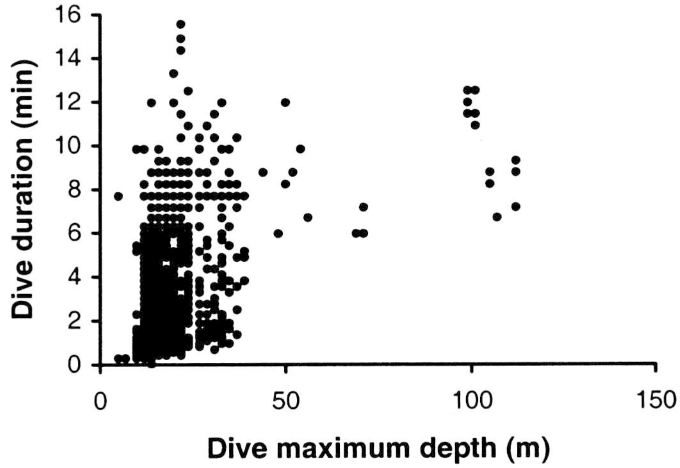

FIG. 2. Plot of dive duration on maximum depth for all whales combined.

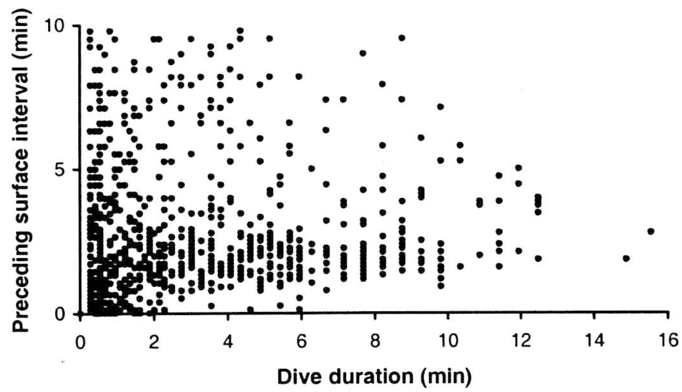

FIG. 3. Plot of surface interval preceding a dive (PSI) on dive duration. Dives with a PSI greater than 10 min have been ignored to avoid sustained periods of rest.

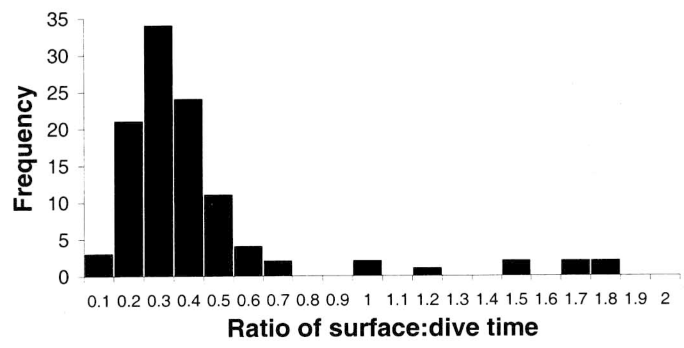

FIG. 4. Frequency distribution of the ratio FSI (following surface interval): dive duration for consecutive dives of at least 5 min. (n = 108, median = 0.30).

exceptional vertical speeds of 2 ms^{-1} over a 40 s interval (Martin and Smith, 1999), and for dives that had two or more consecutive depth measurements made during the descent or the ascent. The sample of such measurements, though small and restricted to the two male belugas, was nonetheless informative: for descent, the mean speed was 1.42 ms^{-1} (range 1.1–1.7, n = 7); for ascent, the mean was 1.73 ms^{-1} (range 1.7–1.8, n = 4).

Dive Sequence (Scale of Hours)

An understanding of behaviour on a scale of hours is given by the variation in proportion of time spent near the surface per 2 hr HIST page. Figure 6 illustrates this, by sex, in both shallow (≤ 25 m) and deeper (> 25 m) marine waters. The shape of the distributions varies between the sexes, but two general observations can be made. First, the whales usually spent a lower percentage of time below the surface (PBS) in any 2 hr period than they were capable of spending, especially in shallow water. Second, despite this, occasional 2 hr periods of intense diving did occur, even in shallow water.

Consecutive 2 hr periods with PBS in excess of 70% were unusual; only male 5800_93 achieved more than two

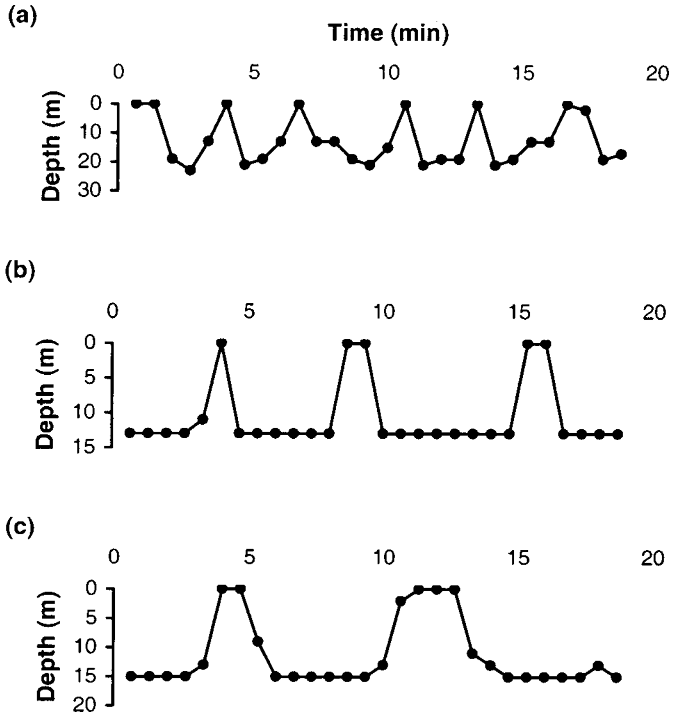

FIG. 5. Time-depth profiles of shallow dives. Profiles (a) and (b), which represent dives of female 5801_93 in shallow water, demonstrate two typical behaviours. Profile (c) represents dives by male 5805_93 in water 100 m deep, showing behaviour that is unusual in deep water.

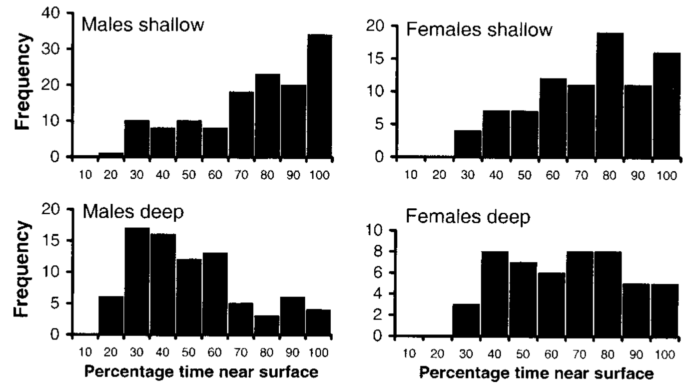

FIG. 6. Frequency distribution of percent time spent near the surface within 2 hr periods in shallow (≤ 25 m) and deeper (> 25 m) marine waters, by sex.

back-to-back at any time (this animal had a PBS greater than 80% for three contiguous periods on 10 August in water about 30 m deep). A closer view of dive behaviour during periods of intense activity was given by SEQuence data. Figure 7 demonstrates four dive bouts during which 75% or more of time was spent below the surface. The best performance recorded overall was by whale 5800_93 during an 87 min period starting at 1515 local time on 10 August (Fig. 7a). Nine consecutive dives (duration 3.8–12.5 min) were made to 22–27 m with 83.9% of the period spent below 4 m depth.

Although the study animals spent a large proportion of time near the water surface, and not all dives were to the seabed or riverbed, it was apparent that these whales did not spend many consecutive hours without diving to the bottom of the water column. The evidence for this was in two parts. First, consecutive dives, and most dives within a sequence (TDR and SEQ pages), were usually to a similar maximum depth. In the overwhelming majority of cases, this depth matched the water depth whenever the whale's location was established accurately. Secondly, the maximum depth recorded within consecutive 2 hr blocks (HIST data) were usually very similar, and again matched water depth when this was known. Exceptions to this pattern stood out, and monotonic increases or decreases in this value invariably reflected the whale's progress from shallow to deep water or vice versa. Quantification of this behaviour was easiest in deeper waters because of the greater absolute difference in depth between a benthic dive and a mid-water dive. In 39 two-hour periods during which water depth was known to be at least 50 m, the whale failed to dive to the seabed within only two periods, and never within two consecutive periods. In other words, during this study the whales rarely spent two hours, and never as many as four, without diving to the seabed.

Diurnal Variation (Scale of a Day)

Variation in two behavioural measures with time of day was investigated with the Kruskal-Wallis test and HIST 2 hr blocks. The data from 2 hr summaries were allocated to a particular hour, approximating to the mid-point of the period. Thus data collected from 0930 to 1130 (mid-point 1030) were assigned to hour 10. No significant diurnal variation was found for any animal either in the proportion of time spent near the surface (PNS) ($p > 0.25$ in all cases) or in the rate of making long (> 5 min) dives ($p > 0.25$).

A direct comparison was also made between day (0200–2200 local time) and night (2200–0200) behaviour, using the same measures and χ^2 tests. Here, no differences were found in the rate of long dives ($p > 0.3$), but there was an indication that some belugas spent a greater proportion of time near the surface after dark (female 5803_93: $p < 0.01$; male 5800_93: $p = 0.06$). The in-river data were then excluded to remove the possibility that this effect was simply due to the whales' spending more time in rivers after dark, but the same result was obtained.

Medium- and Long-term Behaviour (Scale of Days or Weeks)

The response of whales to varying water depth was also examined using the measures of PNS and the rate of long submergences. Plots of PNS on maximum dive depth within 2 hr periods (HIST data) by sex are shown in Figure 8. They demonstrate that when dives are uniformly shallow (and water depth is probably shallow too, see METHODS) the proportion of time spent in the top 4 m of the water column is very variable, from less than 20% to 100%, but in deeper water more time is spent away from the surface zone. This effect was formally tested across

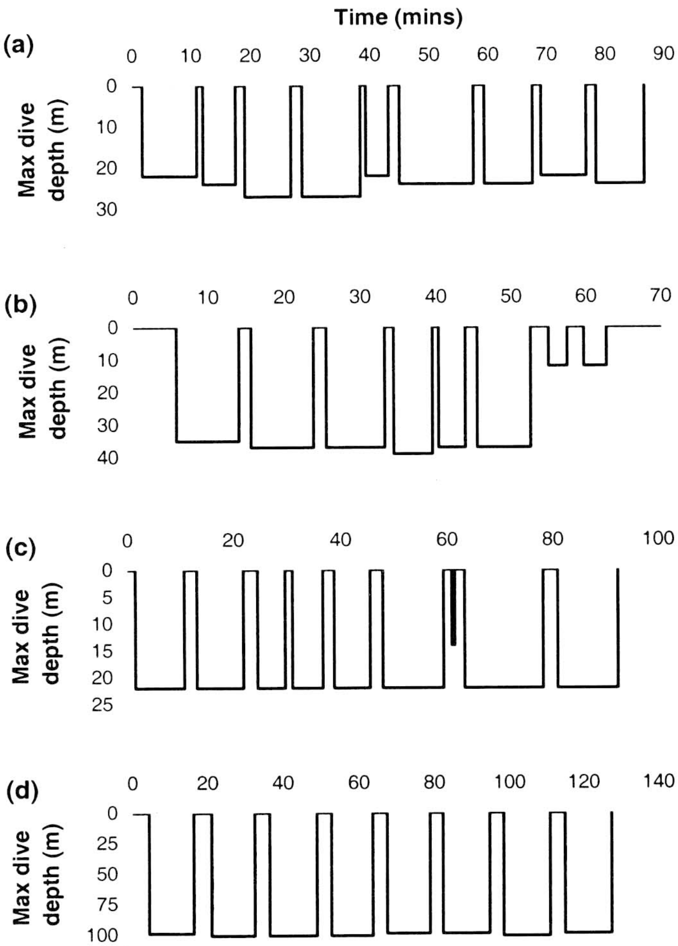

FIG. 7. Surface/subsurface activity during periods of intense diving (less than 25% time spent near the surface). Surface time is shown as a horizontal line at 0 m. All the time spent below the surface in a dive (including descent and ascent) is shown as a horizontal line at the maximum depth of the dive. (a) male 5800_93, on 10 Aug 1993, starting at 1515 local time; (b) female 5801_93, on 27 Aug 1993, starting at 1059 local time; (c) male 5805_93, on 31 Aug 1993, starting at 1022 local time; (d) male 5805_93, on 10 Sept 1993, starting at 0600 local time.

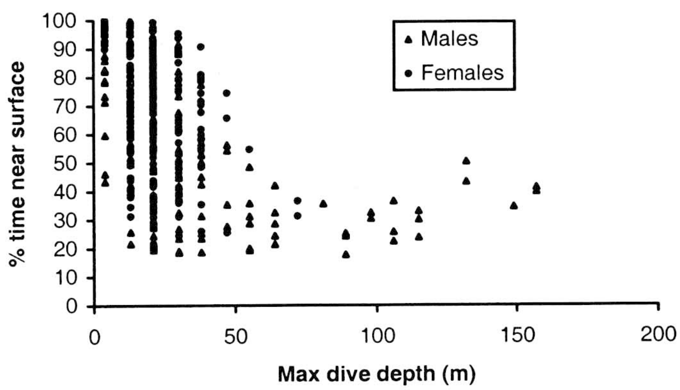

FIG. 8. Plot of percentage time near the surface vs. dive maximum depth within 2 hr periods, by sex. Depths are ± 4 m of true value.

three habitats (riverine, shallow marine (≤ 25 m), and deeper marine (> 25 m), using only 2 hr HIST blocks for which a whale's location was accurately known). Mean and median values of PNS decreased from riverine to shallow to deep waters for the four whales (Table 4a), and the differences were statistically significant for all but female 5801_93 (ANOVA results in Table 4a). The two males and female 5803_93 spent on average more than 92% of their time near the surface in rivers, 59–76% in shallow marine waters, and 45–51% in water more than 25 m deep. Table 4b gives the percentage of time spent by the whales in the upper 9 m of the water column in each habitat, a measure useful mainly for interpreting visual aerial surveys.

The average frequency of long (> 5 min) dives increased successively from riverine to shallow marine to deep marine waters for each animal, but the effect was not significant for female 5801_93 (Table 4c). Neither male made a long dive while in rivers, but both averaged more than 2.3 long dives per hour in deeper marine waters. In contrast, neither female averaged more than 1.1 long dives per hour in any habitat.

Dive Behaviour During the Course of the Experiment

A broad overview of dive behaviour is provided by looking at the maximum depth achieved by the four study animals within 2 hr blocks of time throughout the course of the experiment (Fig. 9). Two characteristics of their behaviour are worth highlighting here. First, few of their dives exceeded 40 m during the month of August, and none exceeded 100 m. Second, a sharp change in dive behaviour occurred at the onset of the autumnal migration in the first few days of September; thereafter, 2 hr periods always (in this sample) included deep dives.

DISCUSSION

Generalization from only four animals in a single year can be misleading, but the consistency of results across the sample allows some confidence that at least the principal conclusions of this study are valid. Furthermore, larger studies of this species at higher latitudes (Martin et al., 1998; Martin and Smith, 1999) have demonstrated that there is relatively little behavioural variation between belugas in a particular population.

Dive durations were generally shorter in this study than those documented for eastern Canadian High Arctic belugas (Martin and Smith, 1999). However, a simple comparison can be misleading because duration is related to dive depth in both populations, and Hudson Bay animals are confined to shallower waters in summer. Data from a sample of dives to more challenging depths (say, more than 300 m) would be necessary to compare the dive capability of Hudson Bay and Canadian High Arctic belugas properly. Even then, the smaller body size of the former population would have to be taken into account.

Although no exceptionally long breath-holds were recorded, the whales frequently remained at shallow depths for more than 5 min, and many times for more than 10 min, even when the commute time to the surface was 20 s or less.

TABLE 4. Characteristics of beluga behaviour in three different habitats. Data are from 2 hr periods during which whales were known to be in either riverine, shallow marine (≤ 25 m), or deeper marine (>25 m) waters. (a) Percentage of time spent in the surface zone (< 4 m); (b) percentage of time spent in the top 9 m of the water column; (c) number of long (> 5 min) dives per 2 hr period. The null hypothesis of the ANOVA test was that there is no difference in the behaviour of each whale between the different habitats.

	ANOVA			Riverine						Shallow Marine						Deep Marine					
Whale No.	DF	F	*p*	Mean	SD	Med.	n (× 2 hr)	Min	Max	Mean	SD	Med.	n (× 2 hr)	Min	Max	Mean	SD	Med.	n (× 2 hr)	Min	Max
a)																					
5800_93	2	43	< 0.001	97.9	4.2	100	7	97.9	100	75.3	23.2	78.3	45	19.6	100	45.3	21.0	41.7	52	18.6	94.8
5801_93	2	1.5	0.22	85.9	23	94.6	8	32.6	100	78.9	19.0	78.7	45	27.3	100	71.0	19.8	74.4	22	25.6	95.3
5803_93	2	61	< 0.001	92.6	16	100	44	32.4	100	58.5	19.8	56.6	36	27.3	100	50.7	16	49.6	27	24.4	90.6
5805_93	2	17	< 0.001	99.7	0.7	100	6	98.5	100	67.2	23.8	71.6	77	20.6	100	46.8	23.6	38.6	30	17.8	91.4
(b)																					
5800_93				99.9	0.3	100	7	99.2	100	89.5	15.0	96.9	45	37.6	100	55.3	23.8	54.4	52	20.3	97.0
5801_93				89.7	23	98.8	8	34.1	100	86.4	15.5	89.9	45	43.0	100	76.6	18.8	82.3	22	29.1	96.1
5803_93				98.0	7.9	100	45	51.8	100	78.9	20.1	85.4	36	34.5	100	62.3	17.1	62.2	27	30.7	92.2
5805_93				100	0	100	6	100	100	83.3	18.1	89.0	77	21.3	100	55.0	25.1	53.1	30	20.9	96.1
(c)																					
5800_93	2	32	< 0.001	0	0		8			1.3	2.3		71			5.5	4		45		
5801_93	2	0.4	> 0.6	1.1	3.2		8			1.7	2.5		59			2.2	3.6		23		
5803_93	2	5.2	< 0.01	0.2	1.1		45			1.2	2		45			1.7	2.9		28		
5805_93	2	17	< 0.001	0	0		7			1.8	2.5		83			4.7	3.3		31		

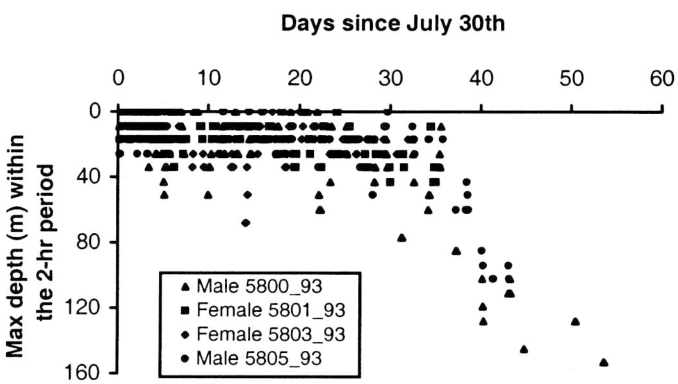

FIG. 9. Time series of the maximum depth achieved within a 2 hr period, by animal.

This implies that the whales were completely comfortable with submergences of these durations, although even the adult males rarely remained below the surface for 12 min or more at any depth. The lack of a relationship between the duration of a dive and that of the surface period on either side of it confirms, as expected, that breath-holds of this magnitude are carried out under normal aerobic metabolism. Such dive durations are approximately what would be expected for cetaceans of their body size, but less than a similar-sized pinniped would be expected to achieve (Schreer and Kovacs, 1997; Martin and Smith, 1999). Another measure of dive capability reported here—the proportion of time spent below the surface during bouts of diving—was equally unexceptional for a medium-sized odontocete. But again, results obtained in shallow water may be misleading; these animals would be expected to improve their performance in deeper water, where commute time is greater and where an advantage could be gained in maximizing time at a target depth.

The clear differences in dive behaviour between the males and females in this limited sample may have been due to differential body size. But in water depths where all adults could explore the entire water column with ease, it is likely that the calf accompanying each female could have had a greater influence. No quantitative studies have yet been carried out to assess the impact of a calf on the behaviour of a wild adult female beluga. However, it seems reasonable to assume that, in caring for a calf with limited diving ability, mothers may spend less time away from the surface zone, avoid deep dives, and perhaps spend more time in sheltered waters. This study has demonstrated that habitat influences key characteristics of dive behaviour, so it would be surprising if the presence of a calf were not reflected in the behaviour of the mother.

The regular and frequent visits to the seabed in all water depths seen in Hudson Bay belugas mirror the behaviour seen in High Arctic animals, and the square-shaped dives seen in deeper waters confirm that whales are simply commuting through the water that separates the seabed and the surface. The flat-bottomed nature of these dives is consistent with the whales' foraging on or very close to the seabed (Martin and Smith, 1999). There is no indication that these animals chase prey vertically in the water column, in the manner of narwhals (Martin et al., 1994). The vertical speeds recorded in this study are well within the range exhibited by High Arctic belugas (Martin et al., 1998), and all indications are that the two populations have similar deep-dive characteristics. The maximum depth in Hudson Bay is ~200 m, and a beluga travelling at the mean measured rates of descent and ascent would take 4.3 min to commute to this depth and return immediately to the surface. Even with a modest breath-hold of 10 min, such depths would still allow more than 50% of the dive duration to be spent on the seabed—more than sufficient time for sustainable foraging behaviour.

This is the first study of beluga dive behaviour at relatively low latitudes and, as such, the first able to compare behaviour during the hours of darkness and daylight in summer. However, apart from an indication that some whales may spend more time near the surface during the hours of darkness (the results were not consistent across all animals), no differences were apparent. We can certainly conclude that there is no sudden cessation or increase in diving with the loss of daylight.

In summary, although the beluga population summering in western Hudson Bay differs markedly in habitat preference to the population studied previously to the north, there are no apparent differences in dive behaviour between the two populations that cannot be attributed to habitat. The dive durations achieved by animals in this study would allow them to forage at much greater depths than they encounter in the coastal waters of their summer grounds; indeed, they would be adequate to allow them to exploit benthic resources throughout the entire Hudson Bay region.

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