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Dive Patterns of Belugas (*Delphinapterus leucas*) in Waters Near Eastern Devon Island

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ABSTRACT. Data were obtained for six belugas or white whales (*Delphinapterus leucas*) instrumented with satellite-linked dive recorders in September-November 1995 in waters near eastern Devon Island, Canada. The mean of the daily maximum depths of dives was 483–665 m for the 31–51 days when maximum depth measurements were taken. The deepest dive recorded was 872 m. Both the dive rate (number of dives per hour to depths > 8 m) and the time at surface (time spent within the uppermost 5 m of the water column) declined from mid-September through mid-October. The four females had significantly elevated dive rates during the nights (2300–0500), whereas the males showed no effects of time of day on the dive rates. Few dives lasted more than 18 min, and most lasted either less than 1 min or for 9–18 min. A trend from short dives to longer dives was noted from mid-September through October, along with a decline in the number of dives to 8–20 m and a corresponding increase in the number of dives to 200–452 m during the same period. The small whales made more dives and had longer times at the surface than the large whales, but they did not dive as deeply or for as long periods as did the large whales. Vertical speeds ranged from 0.5 ms^{-1} to 1.9 ms^{-1} for depths of 52–800 m. These speeds are significantly faster than vertical speeds recorded from narwhals (*Monodon monoceros*).

Key words: beluga, *Delphinapterus leucas*, diving, Devon Island, satellite telemetry

RÉSUMÉ. En septembre-novembre 1995, on a recueilli des données sur six bélugas ou dauphins blancs (*Delphinapterus leucas)* équipés d'enregistreurs de plongée en liaison avec un satellite, dans les eaux proches de la partie est de l'île Devon au Canada. La moyenne quotidienne de la profondeur maximale des plongées était de 483 à 665 m pour les 31 à 51 jours durant lesquels on a mesuré la profondeur maximale. La plongée la plus profonde enregistrée était de 872 m. De mi-septembre à mi-octobre, le taux de plongée (nombre de plongées par heure à des profondeurs > à 8 m), de même que le temps en surface (temps passé dans les 5 m supérieurs de la colonne d'eau) ont diminué. Les quatre femelles affichaient un taux de plongée nettement supérieur durant la nuit (de 23 h à 5 h), tandis que le taux de plongée des mâles n'était pas affecté par le moment de la journée. Peu de plongées duraient plus de 18 mn et la plupart duraient soit moins d'une minute, soit de 9 à 18 mn. De mi-septembre à fin octobre, on a noté une tendance à la hausse dans la durée des plongées, parallèlement à une baisse du nombre de plongées entre 8 et 20 m de profondeur et une augmentation correspondante du nombre de plongées entre 200 et 452 m au cours de la même période. Pour les petits dauphins blancs, le nombre de plongées et la durée des périodes passées en surface étaient plus grands que pour les gros dauphins. Les vitesses verticales allaient de 0,5 ms^{-1} à 1,9 ms^{-1} pour des profondeurs allant de 52 à 800 m. Ces vitesses sont notablement plus rapides que les vitesses verticales enregistrées pour les narvals (*Monodon monoceros*).

Mots clés: béluga, *Delphinapterus leucas*, plongée, île Devon, télémesure par satellite

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INTRODUCTION

The waters along the south coast of Devon and Cornwallis Islands and those surrounding Somerset Island are important summering grounds for belugas, or white whales (*Delphinapterus leucas*). In September, the belugas leave Peel Sound, Barrow Strait, and Prince Regent Inlet and head east toward their wintering grounds (Koski and Davis, 1980; Smith and Martin, 1994). Their departure occurs between late August and early October, and the different pulses of migrating belugas may represent different units of the population, with varied migratory destinations. It has long been believed that most of the belugas that move east through Lancaster Sound in September winter either on the West Greenland fishing banks or in the Baffin Bay North Water (Doidge and Finley, 1993). Of special ecological interest are the belugas that remain in the lead and polynya system of the North Water in northern Baffin Bay and Smith Sound. These whales must remain throughout the winter (November through May) in restricted areas enclosed by heavy pack ice (Freeman, 1968; Finley and Renaud, 1980; Richard et al., 1998a).

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We used satellite telemetry to study the late autumn diving patterns of belugas in the waters surrounding Devon Island where they are believed to winter (Richard et al., 1998a). Martin and Smith (1992) have described diving patterns of belugas in Barrow Strait and Peel Sound in August and early September, when the whales occur either in estuaries or in offshore areas of Barrow Strait and Peel Sound. Belugas in Barrow Strait, where maximum depths range between 150 and 350 m, dove to the bottom and probably did not exceed their aerobic dive limits. Their ascent and descent rates ranged to as high as 2.55 ms^{-1} (Martin and Smith, 1992). Belugas in deeper areas, such as our study area, might be expected to exhibit different diving characteristics than those in Barrow Strait.

The dive data reported here were collected by sampling the ambient pressure every 10 s to categorize certain key parameters, e.g., the number of dives to different depths, their durations, and the time spent in different depth categories. This standardized approach allowed us to compare the dive parameters for belugas of different size or age classes and from different areas. It also allowed us to make comparisons with the other monodontid species: the narwhal (*Monodon monoceros*) (Heide-Jørgensen and Dietz, 1995).

MATERIAL AND METHODS

Six belugas were instrumented with satellite-linked UHF transmitters (Wildlife Computers 1/2 W/SLTDR) at Croker Bay (74˚34′N 82˚55′W) in Lancaster Sound between 12 and 15 September 1995 (Table 1). Details about the area of the live capture operation and the configuration, housing, and attachment of the transmitters are given in Richard et al. (1998b). We recorded the sex and the standard length of all the whales before their release (Table 1). All of the females were accompanied by grey calves two-thirds to three-quarters the length of the adult (i.e., approximately 1 to 3 yrs old; Heide-Jørgensen and Teilmann, 1994). The calves stayed within 10 m of the females during the capture and instrumentation. Some of the calves may have been suckling. For the analyses of the dive data, the six whales were classified into two size categories: one composed of two small females (Nos. 20690 and 20694) and one small male (No. 20696), and the other composed of one large male (No. 20688) and two large females (Nos. 20689 and 20695).

The transmitters had pressure transducers with a range of 0–1000 m that were sampled every 10 s to determine the depth of the whale. The unit, and thus the accuracy of these depth readings, was ± 4 m. Data were collected in four 6 h periods (1700–2300, 2300–0500, 0500–1100, 1100–1700) in local time (Greenwich mean time +5 h). Depth readings were compiled before transmission, so that the information received included data on the number of dives deeper than 8 m in 10 different depth categories (8–20, 20–36, 36–52, 52–100, 100–200, 200–452, 452–600, 600–800, 800–900, > 900 m) for each 6 h period; the frequency of dives in six duration categories (0–1, 1–3, 3–6, 6–9, 9–18, > 18 min) for the 6 h periods; and the time spent at 10 different depth categories (0–20, 20–36, 36–52, 52–100, 100–200, 200–452, 452–600, 600–800, 800–900, > 900 m). The time spent in these depth categories was recorded by tallying the corresponding depth category at each 10 s depth reading. Prior to transmission, the data on time spent in these depth categories were downscaled by the smallest common denominator to keep each category below one byte. The downscaling resulted in loss of precision on the measurement of time spent in depth categories for 2.1% of the observations. This affected mostly those depth categories that had the smallest cumulative times recorded, i.e., the deepest categories. No correction of this bias was introduced.

In addition, the number of seconds spent at or above 5 m depth with an accuracy of ± 1 m was recorded for each 6 h period. The sums were scaled by 90 to fit into one byte before transmission. Thus the total time at the surface (i.e., time spent at depths of 0–5 m) might be underestimated by as much as 90 s (< 1%), whereas surface times shorter than 10 s

TABLE 1. Number of dives per hour during 6 h periods for six belugas during the entire period and during the period 16 September to 17 October, with data from all whales. The temporal changes in dive rate are estimated for 24 h summed during the entire period. Y = dive rate, X = days after instrumentation, and p indicates the significance of the slope of the regressions.

				Entire period					Period from 16/9 to 17/10				
Whale No.	Sex	Body length (cm)	Period 1995 (day/month)	Number of 6 h periods	Mean dive rate	SD	95%CI	Range	Number of 6 h periods	Mean dive rate	SD	95%CI	Temporal change in dive rate during 24 h for the entire period
20688	Male	465	15/9 – 18/10	127	7.4	2.3	7.0 – 7.7	2.5 – 13.7	122	7.4	2.3	7.0 – 7.8	No trend, Y = 7.5 – 0.006X $p = 0.8078$
20689	Female	404	15/9 – 28/10	138	7.5	2.8	7.0 – 7.9	2.5 – 18.8	124	7.6	2.8	7.1 – 8.1	Significant decline, Y = 9.2 – 0.091X $p = 0.0001$
20690	Female	368	13/9 – 17/10	136	10.4	4.7	9.6 – 11.2	3.0 – 31.0	124	10.5	4.7	9.7 – 11.4	Not significant decline, Y = 11.4 – 0.064X $p = 0.1200$
20694	Female	372	16/9 – 30/10	137	6.7	3.0	6.1 – 7.2	2.5 – 21.7	123	6.7	3.1	6.2 – 7.3	Not significant decline, Y = 7.1 – 0.023X $p = 0.3887$
20695	Female	392	16/9 – 03/11	184	6.5	2.5	6.1 – 6.9	2.5 – 20.2	128	6.9	2.6	6.4 – 7.3	Significant decline, Y = 8.4 – 0.069X $p < 0.0001$
20696	Male	408	17/9 – 13/11	211	8.4	2.7	8.0 – 8.8	3.8 – 24.3	124	9.0	3.2	8.4 – 9.5	Significant decline, Y = 10.5 – 0.066X $p < 0.0001$

are missed. We believe that few if any periods when the whale moved within 5 m of the surface lasted less than 10 s. Finally, the maximum depth of dives during 24 h was measured.

The vertical speed of the whales could be inferred from the simultaneously recorded time-at-depth data and number of dives to different depths. This could be done when the destination depth category (i.e., the category with the deepest dive) was isolated from the previous depth categories by at least one transit depth category (i.e., the category through which the animal passed to go to the dive destination category). The isolation of the deepest depth category was necessary to allow the determination of the number of dives that went through the transit depth categories. The time spent in the transit depth categories (TAD) was then used as an estimate of passage time through these depth categories:

$$\text{Vertical speed (ms}^{-1}\text{)} = N \times D / (\sum TAD / 2)$$

where N is the number of dives to the isolated dive destination category, D is the vertical distance (in m) across the transit depth categories to the category with the dive destinations, and TAD is the time-at-depth measurements (in s) through the transit depth categories. The time is divided by two because it includes both ascent and descent times. For example, assume that one whale made four dives to the 600–800 m category, but none to the three categories between 100 and 600 m. Assume that it spent 494 s at 100–200 m, 1059 s at 200–452 m and 635 s at 452–600 m, for a total time of 2188 s. Thus, the vertical dive speed is [4 dives × (600–100) m]/(2188/2) s or 4 × 500 m/1094 s = 1.83 ms^{-1} for the transit depths between 100 and 600 m.

The dive data were obtained from the instrumented whales through the Service Argos positioning and data retrieval system (see Harris et al., 1990).

Bathymetric categories, most in 100 m increments, were extracted from isobath maps (GEBCO, 1977) of the areas where the whales were located.

RESULTS

Maximum Depths of Dives during 24 h

Maximum dives were recorded on 31–51 d for the six whales. The deepest measured dive was to 872 m, and all whales had maximum dives to more than 700 m (Fig. 1). One female (No. 20695) had a significantly deeper mean depth of maximum dives than the other whales (t-test: $p < 0.01$; compare means in Fig. 1). The average of the deepest dives of the large male (No. 20688) and the two large females (Nos. 20689 and 20695) was also significantly deeper (t-test: $p = 0.0006$) than the average of the deepest dives of the small male (No. 20696) and the two small females (Nos. 20690 and 20694).

The bathymetric information on the areas where the whales were diving is coarse, since detailed soundings are missing for most of the area and the contour lines are established through few data points. Furthermore, the maximum dives

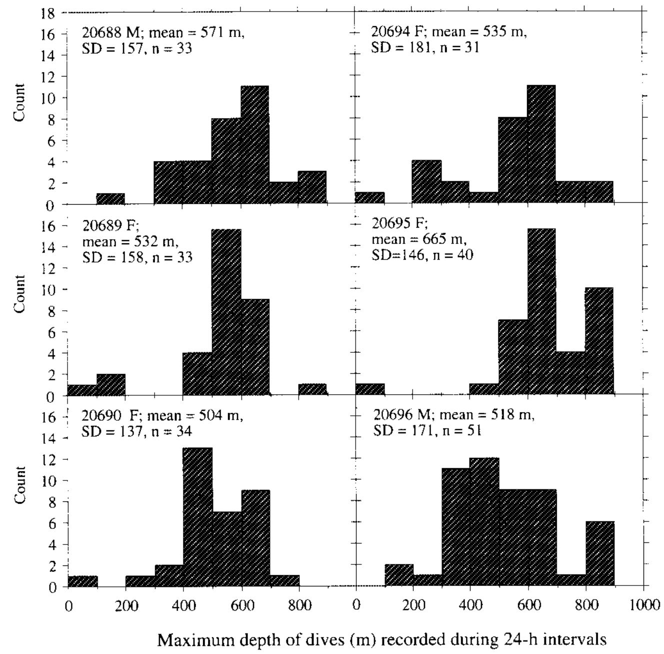

FIG. 1. Distribution of maximum dive depths for six belugas tracked from September to November 1995 in the waters near eastern Devon Island. The maximum dives are measured for 24 h periods.

are recorded over a 24 h period, during which the whales may have moved over considerable distances. It is therefore impossible to establish the exact position where the maximum dive was conducted. Nevertheless, most maximum dives reached the maximum seafloor depths indicated on bathymetric maps. Few maximum dives spanned less than 70% of the maximum depth of the water column, and most probably went all the way to the bottom (Fig. 2). The deeper the maximum dives, the smaller was the relative difference between maximum seabed level and maximum dive depth (maximum seabed level - maximum dive depth/maximum dive depth; ANOVA for arcsine transformed ratios $p < 0.0001$).

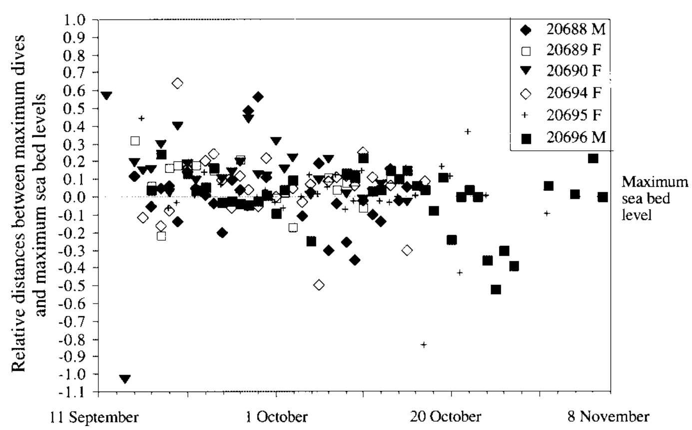

FIG. 2. Temporal variations in distance of maximum dives from maximum seabed levels for six belugas. The maximum dives are measured for 24 h periods and the maximum seabed levels are estimated from bathymetric charts with the positions of the whales during the 24 h when the maximum dives were recorded. The y-axis shows the distances of the maximum dives from the ratio between maximum dives and maximum seabed levels; ratios below 0 indicate that the whales went deeper than the maximum depth the bathymetric charts indicate.

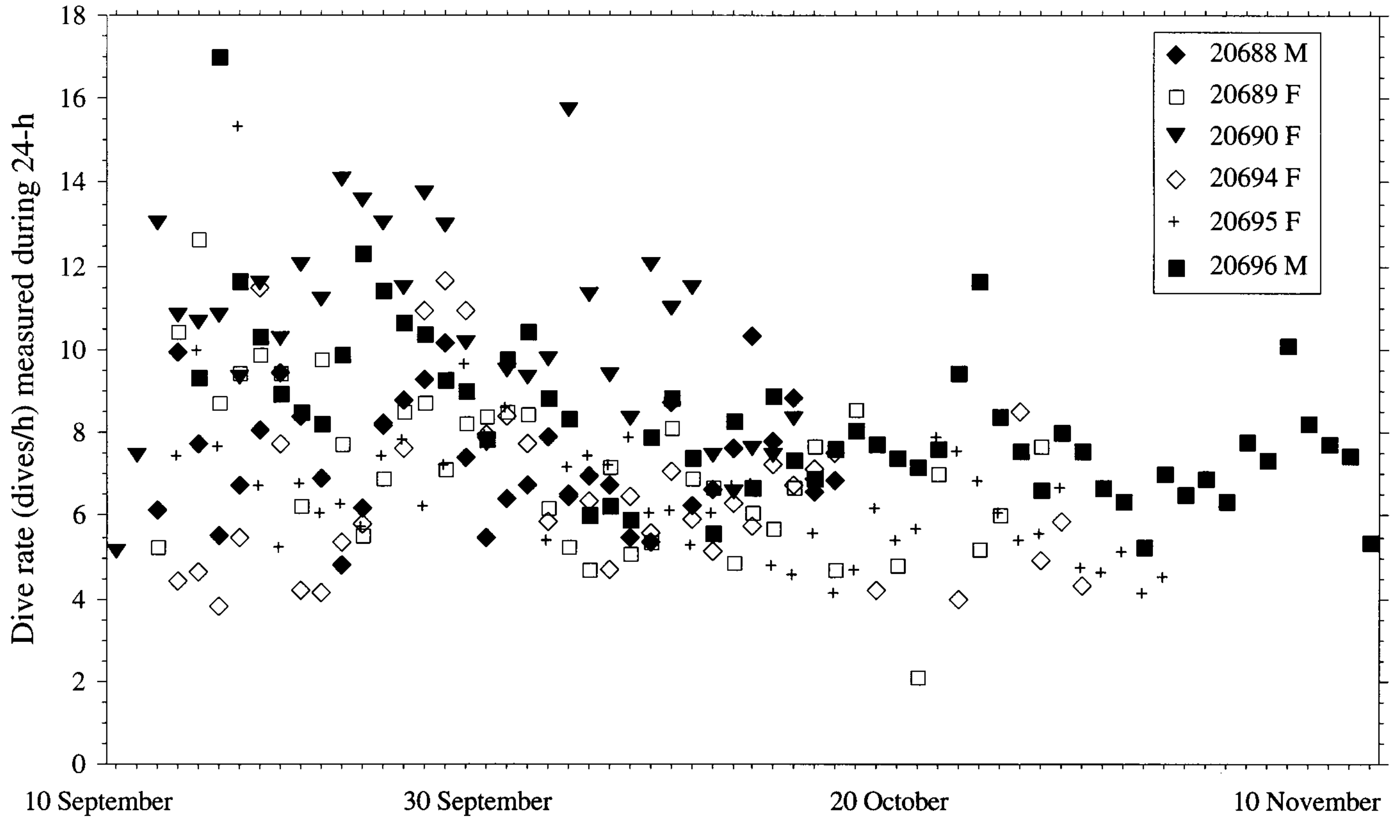

FIG. 3. Dive rate (number of dives per hour summed over 24 h) plotted against date for six belugas from September to November.

Number of Dives per Hour

At least five whales showed a declining dive rate (number of dives per hour made to depths greater than 8 m) during the data collection period (Fig. 3). For three whales, regressions of both all 6 h periods against day and the sum of dives during 24 h against day showed a significant decline (Table 1). The mean dive rates of the whales were compared for the period 16 September through 17 October, during which data from all six whales were available. The mean dive rate clearly varied among the whales: one small female (No. 20690) had a significantly higher dive rate (t-test: $p < 0.0001$) than any of the other whales, whereas another similar-sized female (No. 20694) had the lowest dive rate (Table 1). The three small whales (Nos. 20690, 20694, and 20696) had a significantly higher mean dive rate (mean = 8.8, 95% CI: 8.3–9.2) than the three large whales (mean = 7.3, 95% CI: 7.0–7.5) when compared during the period with observations from all six whales. After mid-October, the mean dive rate was slightly but not significantly higher in the small whales although some individual differences remained significant. The overall mean dive rate for all six whales was 6.8 dives per hour (95% CI 6.5 –7.0) after mid-October.

Diurnal Differences in Number of Dives

The two male belugas (Nos. 20688 and 20696), considered together, showed no effect of the time of day on the dive rate (ANOVA, $p = 0.7630$), whereas the four females, considered

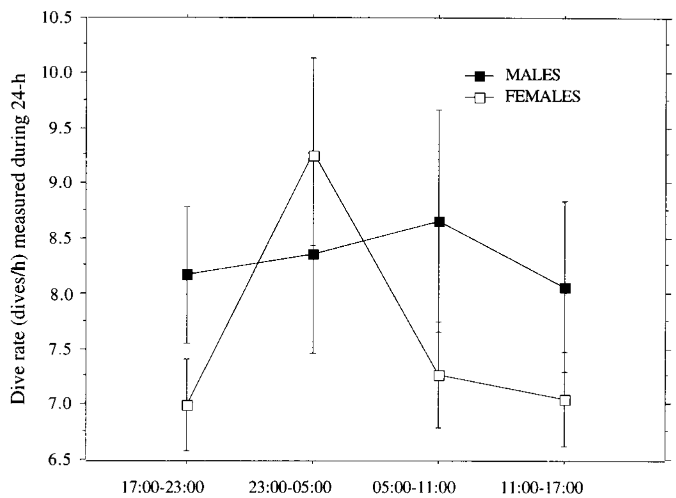

FIG. 4. Diurnal variations in dive rates (number of dives per hour) for male and female belugas. The dive rates are measured during four 6 h periods. Vertical lines indicate 95% confidence intervals.

together, had a significantly elevated dive rate during the hours between 2300 and 0500 (ANOVA, $p = 0.0001$, Fig. 4).

Time at Surface

Time spent in the upper 5 m of the water column is referred to as "surface time" for convenience. Surface time showed no relationship with time of day (6 h period, ANOVA, $p = 0.15$), but all six whales had significantly higher surface times from

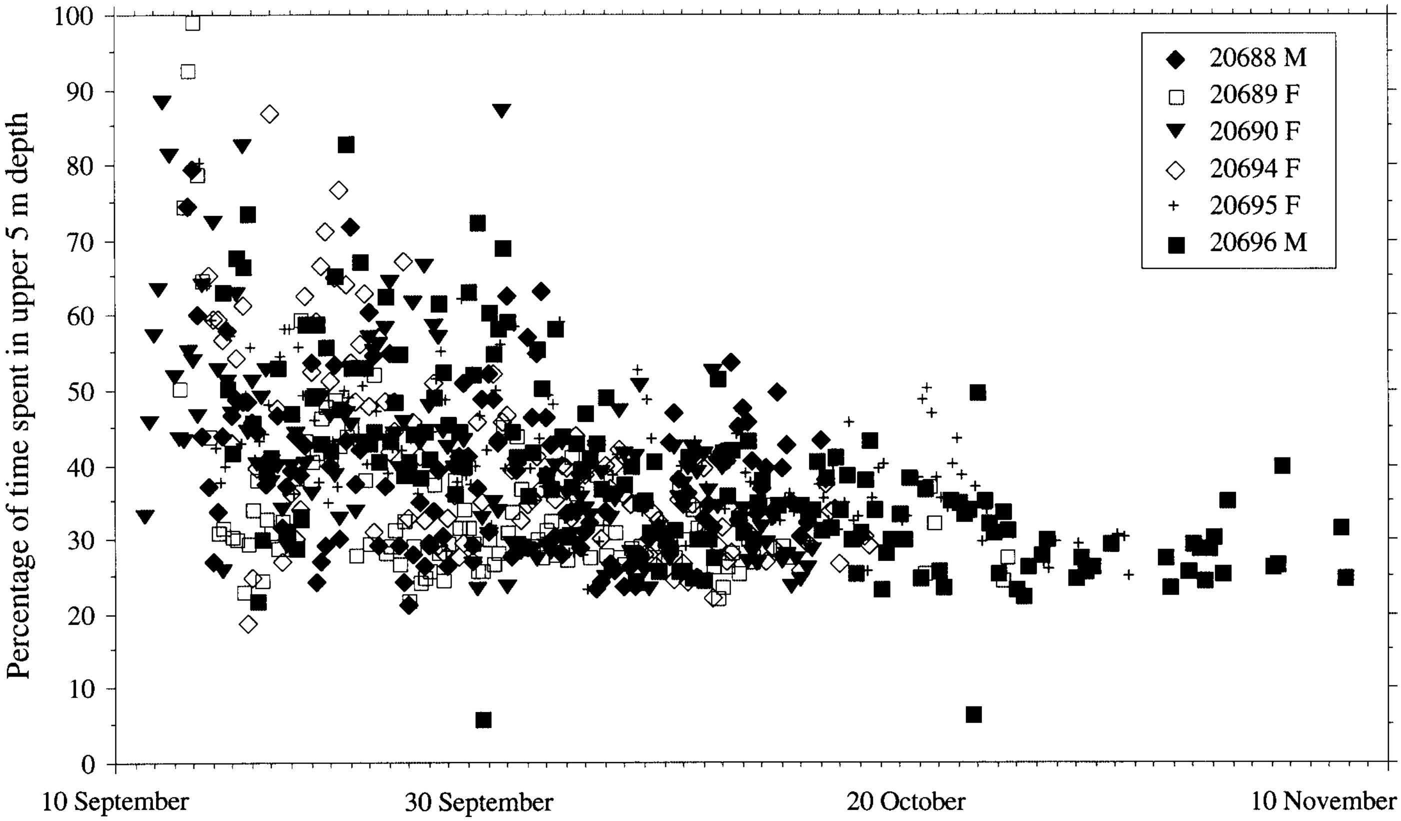

FIG. 5. Surface time (percentage of time spent at 0–5 m depth) plotted against date for six belugas from September to November. The two dots below 20% are probably errors, as less than 0.5% of the measurements on all the six whales were below 20%.

TABLE 2. Surface time (percentage of time spent in the upper 5 m of the water column) for six belugas and the estimates of the rate of decline in surface time during September-November. Y = surface time, X = days after instrumentation, and *p* indicates the significance of the slope.

Whale No.	Sex	Period (day/time)	Number of 6 h periods	Mean	SD	95% Cl	Range	Temporal change in surface time
20688	Male	15/9 – 18/10	122	39.6	11.1	37.6 – 41.6	21.3 – 79.6	Y = 45.5 – 0.3X, $p = 0.0044$
20689	Female	15/9 – 27/10	118	34.4	12.4	32.1 – 36.7	21.7 – 99.2	Y = 45.3 – 0.6X, $p < 0.0001$
20690	Female	12/9 – 17/10	128	41.2	13.4	38.8 – 43.5	22.9 – 87.9	Y = 54.8 – 0.8X, $p < 0.0001$
20694	Female	16/9 – 20/10	116	39.8	13.0	37.4 – 42.1	18.8 – 86.7	Y = 57.2 – 0.9X, $p < 0.0001$
20695	Female	16/9 – 02/11	156	40.1	9.2	38.7 – 41.6	22.9 – 80.0	Y = 50.6 – 0.4X, $p < 0.0001$
20696	Male	17/9 – 13/11	172	38.9	12.7	37.0 – 40.8	5.9 – 82.9	Y = 53.9 – 0.5X, $p < 0.0001$
Total			812	39.1	12.1	38.2 – 39.9	5.9 – 99.2	Y = 49.7 – 0.5X, $p < 0.0001$

mid-September through early October (ANOVA, $p = 0.0001$). During 40 d in the autumn, their surface time was reduced by about half (see Fig. 5). Out of a total of 812 estimates of surface times obtained from the six whales, only three surface times constituted less than 20% of an entire 6 h period. The overall mean for all six whales during the study period was 39% (Table 2), and the asymptote of the decline approaches 20% (Fig. 5). These percentages suggest that at least 20% of the whales' time was spent at or above 5 m of depth but that there was a strong temporal trend in the surface time.

There were slight differences among the six whales in both their mean surface time and the intercept of the regression of surface time with number of days after instrumentation (Table 2). The three large whales (Nos. 20688, 20689, and 20695) had lower intercepts and slopes of regressions of surface time versus total tagged time than the other whales. Also the mean of their surface time was lower, but not significantly lower, ($p = 0.064$) than the mean of the three small whales (Nos. 20690, 20694, and 20696).

The correlation between mean daily surface time and mean daily speed, determined from consecutive positions in intervals of 0.5 to 2 h between positions, was tested using data on swimming speed from Richard et al. (1998b). No correlations were found, and the swimming speeds of the whales seemed to be independent of the time spent in the upper 5 m of the water column.

Depths of Dives

None of the whales made dives deeper than 900 m, and all had few dives (5% or less) to depths greater than 600 m. Most diving activity was directed towards the depth

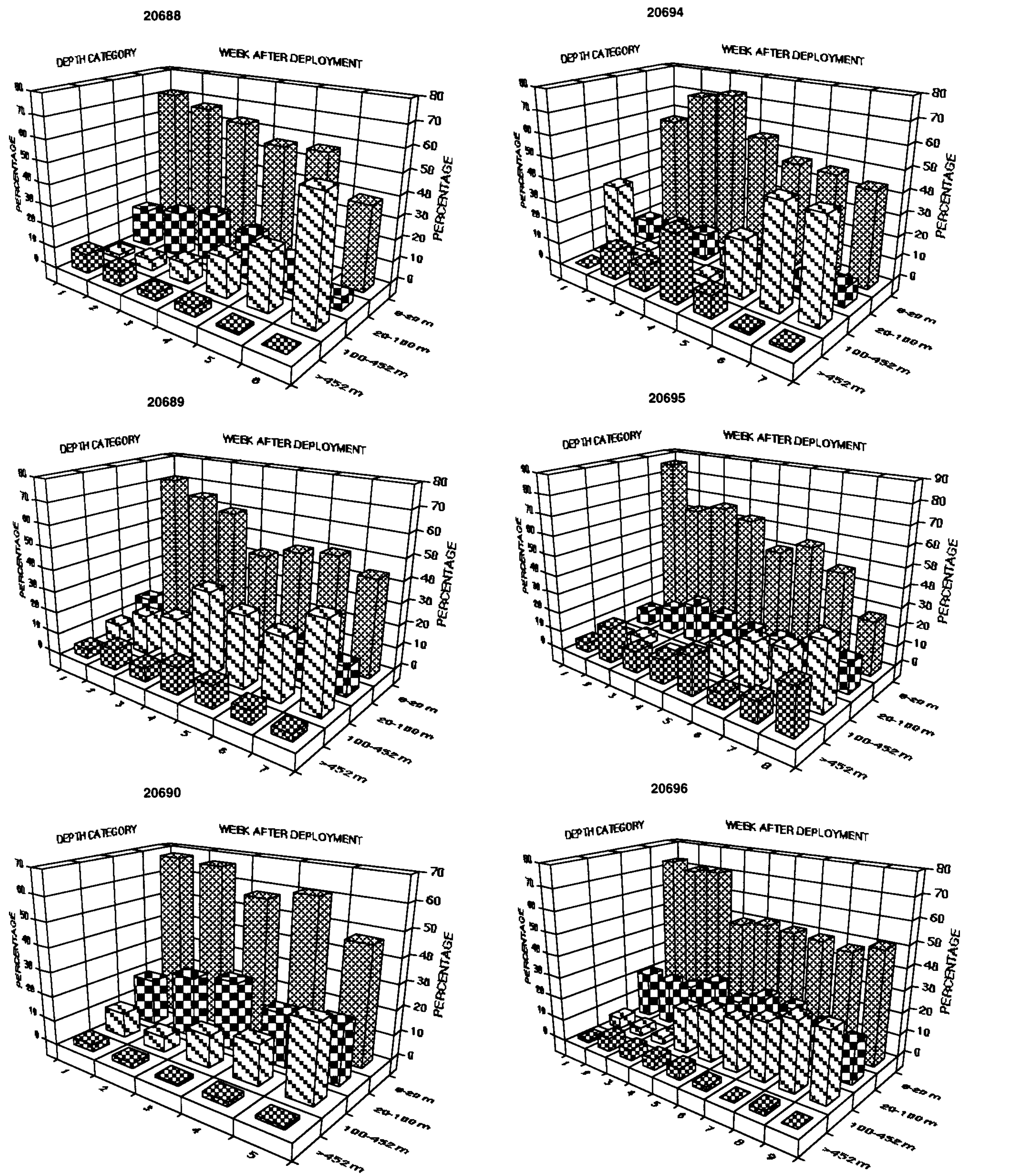

FIG. 6. a-f. Proportional distribution of dives to four depth categories for 6 to 10 weeks after deployment.

category just below the surface (8–20 m) or to the depth category between 200 and 452 m. There was a declining trend with time for all six whales in the proportion of dives to the first 8–20 m (ANOVA, $p < 0.05$). The temporal decline in dives to this near surface category was accompanied by a corresponding increase in dives to the deeper categories between 200 and 452 m (ANOVA, $p < 0.006$). After week 5, three of the whales also had a decline in (or a complete absence of) dives to depths greater than 452 m (see Fig. 6).

TABLE 3. Trends in durations of dives from mid-September through October for six belugas. *p* indicates significance of slope (β), and a is the intercept.

	0 – 1 minute dives			1 – 3 minute dives			3 – 6 minute dives			6 – 9 minute dives			9 – 18 minute dives		
Whale No.	β	a	*p*	β	a	*p*	β	a	*p*	β	a	*p*	β	a	*p*
20688 M	-0.16	17.1	0.0583	-0.04	10.2	0.4907	-0.08	9.6	0.1534	0.10	3.1	*	0.21	2.3	***
20689 F	-0.40	18.0	***	-0.31	17.2	***	-0.11	10.1	*	0.10	2.4	***	0.21	7.0	***
20690 F	-0.46	32.0	*	-0.07	17.5	0.4827	-0.13	13.6	0.1422	0.12	2.1	**	0.25	2.2	***
20694 F	-0.29	17.1	**	-0.10	10.9	0.0528	-0.04	8.2	0.4499	0.12	0.4	***	0.23	4.9	***
20695 F	-0.37	20.4	***	-0.22	14.8	***	-0.05	8.5	0.0683	0.10	0.9	***	0.20	3.0	***
20696 M	-0.43	31.1	***	-0.17	15.6	***	-0.04	9.9	0.0576	0.03	3.3	*	0.20	3.6	***

*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.005$

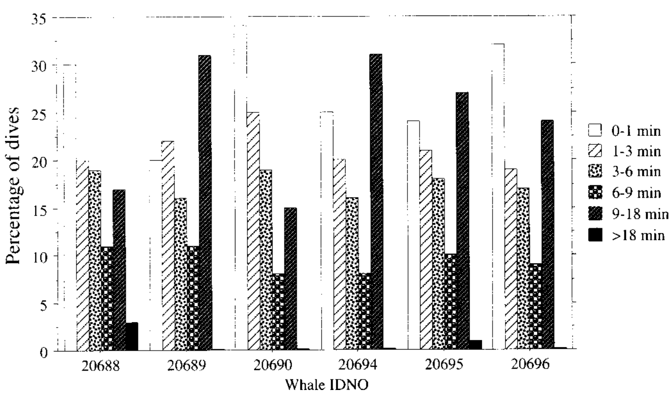

FIG. 7. The proportional distribution of 43 764 dives to different duration categories for six belugas.

We lost contact with the two males when they were located over a bank southeast of Ellesmere Island, where water depths are around 200 m. During the last week before contact was lost, an average of 16% (No. 20688) and 21% (No. 20696) of their dives were to the depth category of 200–452 m, and few dives deeper than 452 m were recorded.

The last positions of the four females were east and southeast of Devon Island, in areas where the depth to the sea bottom averages about 400–500 m. Unlike the males, the females had 30% or more of their mean weekly dive activity in the 200–452 m category. One of them (No. 20695) had 27% of her dives to depths of 452–600 m.

As one would expect, there was a highly significant correlation between the time spent at different depth categories and the number of dives to those depth categories (ANOVA, $p < 0.001$).

Duration of Dives

The number of dives that lasted less than 6 min declined from mid-September through October for all six whales. During the same period, the number of dives lasting 6–18 min increased. Although these trends were evident for all the whales, they were not always significant (Table 3).

Most dives lasted less than 3 min or between 9 and 18 min (Fig. 7). One whale (No. 20690) tended to allocate most of her dive activity to dives lasting less than 6 min. Out of a total of 43 764 dives for which duration was recorded, only 262 lasted more than 18 min. Of these, 154 were made by the bigger male (No. 20688: 2.8 % of all his dives) and 73 by the biggest female (No. 20695: 1.0% of all her dives). For the other four whales, less than 0.1% of their dives lasted more than 18 min.

The three large whales (Nos. 20688, 20689, and 20695) made significantly more dives of long duration (> 9 min) than the small whales (Nos. 20690, 20694, and 20695: t-test, $p = 0.0017$).

Speed of Vertical Movements

The vertical speed of the whales was significantly dependent on the destination depth and the vertical distance of the dive over which the dive was calculated (ANOVA, $p < 0.0001$, Fig. 8). Vertical distance was also well correlated with the destination depth of the dive ($r^2 = 0.80$). The vertical speeds ranged from about 0.5 ms^{-1} to more than 2 ms^{-1} (Table 4). The slower speeds were probably underestimates in some cases due to the exaggerated effect of the 10 s sampling time on dives of short duration.

An analysis of the effect of whale size on the vertical speeds, with the destination depth as covariate, revealed a significant difference of the slopes of the regressions for the two size groups (ANCOVA, F = 4.98, $p = 0.03$). The three small whales (Nos. 20690, 20694, and 20696) were faster for deep dives (> 350 m) but slower for shallow dives than the three large whales (Nos. 20688, 20689, and 20695; Fig. 8).

A similar significant difference in slope was evident when comparing the vertical speeds of narwhals and belugas, with destination depth as the covariate (ANCOVA, F = 14.94, $p = 0.0001$). Compared to narwhals, the belugas exhibited faster vertical movements at the same depth intervals, but the difference in speed decreased with increasing destination depth (narwhal data from Heide-Jørgensen and Dietz, 1995; Table 4).

DISCUSSION

There was a clear change in dive patterns over the 5 to 8 weeks in which we monitored the diving patterns of the whales. From early October on, all whales reduced the amount of time that they spent at the surface. They also reduced their dive rate and redirected their diving activity from the depth category just below the surface (8–20 m) to

TABLE 4. Vertical speeds during dives to different depths for six belugas and four narwhals. Data on narwhal speeds from Heide-Jørgensen and Dietz (1995).

Vertical distance of dives (m)	Beluga			Narwhal		
	No. of dives	Mean vertical speed (ms^{-1})	SD	No. of dives	Mean vertical speed (ms^{-1})	SD
052	2	0.50	0.13	–	–	–
100	11	1.45	0.56	1	1.09	–
200	141	1.55	0.29	2	1.04	0.07
452	83	1.82	0.24	15	1.14	0.35
600	64	1.87	0.33	4	1.41	0.43
800	9	1.90	0.35	12	1.45	0.50
900	–	–	–	45	2.08	0.19

deeper categories, especially that of 200–452 m. This latter change in preferred depth of dives seems to be related to a change in the type of habitat that they were occupying. At the time when we lost contact with the whales, they were on banks either east or southeast of Devon Island, or southeast of Ellesmere Island (Richard et al., 1998b). These results indicate that the whales were using most of the water column, made daily dives to the bottom, and adjusted their dive activity to the depths of the water masses where they were found. The whales located in deeper waters had a preponderance of dives to the deeper depth categories (200–452 m and deeper), whereas those in shallow waters had a smaller proportion of dives in those depth categories. The whales made at least one dive to the bottom daily, presumably to reach food resources near the bottom.

Belugas are known to winter in leads and polynyas east and south of Devon Island, an area known as the North Water (Finley and Renaud, 1980; Richard et al., 1998a). Because the whales shed the satellite-linked dive recorders anchored to the dorsal ridge within 5 to 8 weeks after its deployment, we were unable to monitor the winter diving of belugas in the North Water. However, since the whales that we studied stayed in the areas where belugas have been seen in spring in the polynya (Finley and Renaud, 1980; Richard et al., 1998a, b), we believe that the diving behaviour described in this study is representative of at least the autumn and early winter diving of those animals that overwinter in the North Water.

The extent and thickness of the pack ice surrounding the North Water probably prevent the belugas from leaving this region for most of the winter. Since the North Water is restricted in size, it can be inferred that the horizontal activity of the whales is reduced in comparison with the open-water season, when they can move more freely. In fact, the reduction in horizontal activity coincides with the thickening of ice cover in early October (Richard et al., 1998b). Thus the reduction in time spent near the surface (< 5 m) probably reflects the fact that the whales are more stationary, perhaps resting or foraging in deeper and more saline water layers. The increased number of dives to the 200–452 m depth category suggests that the belugas depend on food resources found at these depths.

Another monodontid, the narwhal, inhabits the same waters—but not necessarily the same localities—as the

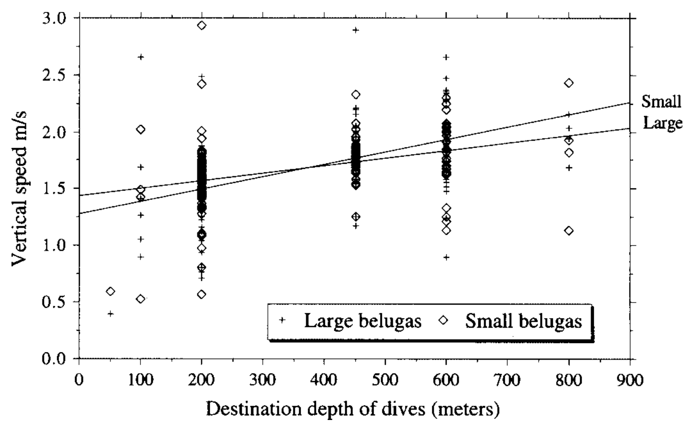

FIG. 8. Correlation between vertical speed and the destination depth of dives for two size groups of belugas. The slopes of the two regression lines were significantly different (ANCOVA, F = 4.98, $p = 0.03$).

belugas. Narwhals tend to reduce their time at the surface between 1 October and 1 December and to maintain a surface time of approximately 20% during winter (Heide-Jørgensen and Dietz, 1995). Some narwhals also reduce their dive rate to a mean of 6 dives per hour after 1 November, behaviour similar to that of the belugas. Both monodontid species reduce their horizontal (see Dietz and Heide-Jørgensen, 1995) and vertical activities and redirect their diving towards deeper depths in winter. The general reduction in dive activity could be a way of conserving energy. The tendency to make deeper dives may also be a consequence of the fact that the whales are simply more stationary during late fall and winter because of the ice.

The fact that the time spent at 0–5 m for these belugas converges towards 20% during the winter has important implications for the interpretation of visual or photographic winter surveys of belugas. Richard et al. (1994) found that models of belugas could not be distinguished to species at depths greater than 5 m. Results from this study suggest that only a fifth of the population would be available above 5 m at any given instant during a winter survey. This adds to the evidence that the winter stock of belugas in the North Water is several times larger than what has been estimated from visual surveys (Finley and Renaud, 1980; Richard et al., 1998a). Also, if belugas spend a similar proportion of their time near the surface off West

Greenland during winter, then the actual abundance there could be several times larger than the abundance estimated at the surface from the aerial surveys (Heide-Jørgensen et al., 1993; Heide-Jørgensen and Reeves, 1996).

There seemed to be differences, albeit not always significant, between the dive patterns of small and large whales. Our study included a male and two females in each size group. The small whales generally made more dives but to lower daily maximum depths, and they had longer surface times than the large whales. They also had fewer dives of more than 9 min duration. For deep dives the small whales moved faster, which would increase their time at depth for their short-duration dives. Diving capacity depends on body volume or weight rather than on body length (e.g., Kooyman 1989). Our measurements of length of whales can be converted to weight by power functions provided by Heide-Jørgensen and Teilmann (1994) or Stewart (1994). If the weight at physical maturity is assumed to be approximately 1 tonne for females and 1.5 tonnes for males, then the three small and the three larger whales have body weights, on average, of 62% and 76%, respectively, of their weights at physical maturity. This difference may well explain the differences in dive patterns.

The vertical speeds presented here for belugas and in Heide-Jørgensen and Dietz (1995) for narwhals combine ascent and descent rates and are calculated as travelling speeds over vertical distances up to 800 m. Faster vertical speeds can be expected over shorter distances and if descent rates are considered separately (Martin and Smith, 1992, Martin et al., 1994). Slower vertical speeds are expected for ascent rates alone, or when the direction of a dive changes within a depth category.

Martin and Smith (1992) reported ascent and descent rates for belugas diving to 350 m. Details on speeds at different depths and on statistics of estimates were not given, but their average and maximum speeds were similar in magnitude to the vertical speeds reported here for belugas diving to similar depths.

Martin et al. (1994) found that one adult female narwhal diving to relatively shallow depths (< 260 m) averaged 1.5 ms^{-1} for descent rate and 1.4 ms^{-1} for ascent rate. Even though some of the vertical speeds behind these averages were measured directly with a velocity sensor over periods of variable length, they were still faster than the swim speeds reported for narwhals (in this study and Heide-Jørgensen and Dietz, 1995), but similar to our values for the belugas (this study). However, the differences in destination depths, distance of dives over which speed is measured, and sampling protocols render the comparison with Martin et al. (1994) difficult.

In a comparable study, narwhals have been documented to dive to depths greater than 1000 m and to have ascent and descent times of 1–2 ms^{-1}, increasing with the destination depth of the dive (Heide-Jørgensen and Dietz, 1995). The belugas that we tracked did not dive deeper than 900 m, but this may only reflect the fact that they were located in shallower waters. Both the narwhals and the belugas made few dives lasting more than 18 min, but the belugas had faster ascent and descent rates than the narwhals. Thus belugas are potentially able to spend more time at depth than narwhals at similar diving depths.

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