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Surfacing Times and Dive Rates for Narwhals (*Monodon monoceros*) and Belugas (*Delphinapterus leucas*)

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ABSTRACT. Time spent at and near the sea surface was measured for 25 narwhals, *Monodon monoceros*, and 39 belugas or white whales, *Delphinapterus leucas*, in West Greenland and Canada from 1993 through 1999, using satellite-linked data recorders. Narwhals spent less time at the surface than belugas did, and the surfacing time of belugas also varied between localities. No clear differences in surfacing time were associated with the time of day, but belugas tended to make more dives during the night than during the day. Despite large variability in surfacing behaviour among individual whales, time spent at the surface by both species declined from August through November. The few data collected from narwhals from November to February indicate that surfacing times remained low during this period although more than 25% of each 6 h period was spent at the surface. Whales made between 2 and 20 dives per hour, and narwhals made significantly fewer dives than did belugas, for which number of dives varied with locality. The number of dives deeper than 8 m declined substantially during the autumn for belugas and narwhals that were moving offshore. When travelling, the whales apparently made fewer dives than at other times.

Key words: Baffin Bay, behaviour, belugas, dive rate, narwhals, surfacing time

RÉSUMÉ. De 1993 à fin 1999, on a mesuré le temps passé à la surface de la mer ou près de celle-ci par 25 narvals, *Monodon monoceros,* et 39 bélougas ou baleines blanches, *Delphinapterus leucas,* dans le Groenland occidental et au Canada, en recourant à des enregistreurs de données en liaison avec un satellite. Les narvals passaient moins de temps que les bélougas à la surface, et le temps passé par ces derniers en surface variait d'un endroit à un autre. Aucune différence marquée dans le temps de surface n'a été associé avec le moment de la journée, mais les bélougas avaient tendance à faire plus de plongées la nuit que le jour. Malgré une grande variabilité dans le comportement de surface parmi les baleines prises individuellement, le temps passé en surface par les deux espèces a diminué d'août à fin novembre. Les quelques données provenant des narvals de novembre à février indiquent que, durant cette période, les durées à la surface sont restées brèves, même si plus de 25 p. cent de chaque période de 6 h se passait en surface. Les baleines effectuaient de 2 à 20 plongées par heure, et les narvals effectuaient un nombre de plongées bien moindre que celui des bélougas, pour lesquels le nombre de plongées variait selon l'endroit. Au cours de l'automne, le nombre de plongées effectuées à plus de 8 m de profondeur diminuait sensiblement pour les bélougas et les narvals qui se déplaçaient au large. Il semble que, lorsqu'elles se déplaçaient, les baleines effectuaient moins de plongées qu'à d'autres moments.

Mots clés: baie de Baffin, comportement, bélougas, taux de plongée, narvals, temps passé en surface

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INTRODUCTION

A whale's time can be divided roughly into time spent at the surface and time spent diving. We refer to the former as the 'surfacing time.' However, 'surfacing' has to be defined more precisely according to the method of measuring surfacing time. Aside from the well-defined breaking of the air/water interface, whales engage in a number of activities that can be interpreted as related to the surface. These include milling, circling, spy hopping, tusk displays for narwhals, and various directional movements (e.g., Pilleri, 1983; Smith et al., 1994). All of these activities can be considered distinct from diving as long as a certain depth threshold is not exceeded. Thus 'surfacing time' is best defined as the time during which the whales are either at the surface or shallower than a certain threshold depth. Similarly a whale's behaviour below the surface can be classified in relation to its diving activity by

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defining 'diving' as submergence below this threshold depth.

Estimating surfacing time is important for correcting counts of whales made during aerial or boat surveys to account for diving whales and for understanding how the whales use various habitats during different seasons. Using models, experiments have shown that adult belugas or white whales, *Delphinapterus leucas*, can be identified on aerial photographs down to 5 m below the surface (Richard et al., 1994). Adult narwhals, *Monodon monoceros*, however, could only be identified with certainty within 2 m of the surface. For both species, juveniles could be reliably identified only when shallower than 2 m. An understanding of geographic and seasonal changes in surfacing patterns for both species is therefore critical, as different correction factors must be applied depending on the circumstances of the survey.

To provide information relevant to interpreting and correcting aerial survey estimates of density or abundance of belugas or narwhals, we collected data on surfacing times for both species in Canada and Greenland from 1993 through 1999. This article describes the sources of variability in surfacing times for narwhals and belugas. We also include some previously published data (Heide-Jørgensen and Dietz, 1995; Heide-Jørgensen et al., 1998) to allow comparison with more recent, larger data sets.

MATERIAL AND METHODS

Instrumentation of Whales

Twenty-five narwhals and 39 belugas were captured and instrumented with satellite-linked data recorders at localities in Canada and Greenland during summer and early autumn (Table 1). Narwhals were instrumented at two localities: Melville Bay and Tremblay Sound (Fig. 1). Belugas were instrumented at three localities: Somerset Island, Devon Island, and Cumberland Sound (Fig. 2). Standard length, sex, and presence of newborn calves (less than 3 months old) were recorded for each whale. See Dietz and Heide-Jørgensen (1995), Dietz et al. (2001), Orr et al. (2001), and Richard et al. (1998, 2001) for details about capturing operations and the configurations of the data recorders.

Collection of Dive Data

Data on diving behaviour were collected following the procedures described in Heide-Jørgensen and Dietz (1995) and Heide-Jørgensen et al. (1998). The number of seconds spent shallower than a depth threshold of either 5 m (± 1 m) or 6 m (± 2 m) was recorded for each of four 6 h periods daily (Table 1). The sums were scaled to a multiplier of 90 s to fit into one byte (< 256) 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 surfacing times of less than 10 s (the sampling frequency) would have been missed.

For 11 belugas tagged at Somerset Island in 1996, the total surfacing time (0–6 m) was divided among time spent dry at the surface (0 m), time between 0 and 2 m depth, time at 2 to 4 m, and time at 4 to 6 m. For each of these four depth categories, the time was recorded as increments of 10 s. Before transmission, the number of 10 s periods was scaled down to keep each category smaller than one byte. The four categories are additive, and the sum represents the time between 0 and 6 m, which is comparable to the surfacing times derived from the other transmitters. The accuracy of the depth readings from these whales was ± 2 m (0.2% of the maximum reading of the pressure transducer).

The dive rate (number of dives per hour) was determined from the number of dives deeper than a certain threshold (usually 8 m, but see Table 1 for exceptions) averaged over either 6 h or 24 h.

The days of the collection of the data were enumerated from 1 January (= day number 1). For the transmitters that continued functioning into a second calendar year, the second year continued with day number 366.

There was a clear effect of day number on the surfacing times, so analysis of variance between different parameters was usually conducted with day number as a covariate (ANCOVA). Unless otherwise stated, significance was determined at the level of $p = 0.05$. Slopes of linear regressions are shown as β.

Elimination of Errors and Extreme Values

The large amount of data collected inevitably contains errors. These can emerge anywhere in the process, as the data are being collected on the whale, as the data are being compressed before transmission, during transmission and reception, during processing by Service Argos, and during data preparation before the analysis. Obvious errors that could be identified easily either were corrected, or the data stream was omitted. For the dive rates, extreme values were eliminated by choosing a limit of 20 dives per hour as a maximum for this parameter. Less than 2% of all the dive rates were more than 20 dives per hour (Fig. 3), and it seems unlikely that the whales ever exceeded this rate (see section on dive rates). Using a similar criterion of omitting the lower 2% of the surfacing times (within 0–5 m) gave a cutoff at 23% of the time spent at the surface for belugas and 20% for narwhals (Fig. 4, see section on surfacing times).

RESULTS

Spatial Dispersal of the Whales

The whales that provided data for the present study were tracked by satellite for 2–162 days as they moved

TABLE 1. Whales used in the present study (total sample size is 11 442 6 h periods). ID # = identification number for each whale. T after the ID # indicates that the transmitter was attached to the tusk; all other transmitters were mounted on the back of the whale. M = male, F = female, +F = female accompanied by a calf. Surfacing depth is the depth to which the surfacing time was measured. Period indicates the days of the year on which data were collected. Dive rate depth is the depth below which the dive rate (dives/h) was measured.

Tagging Site and Year	ID #	Sex	Surfacing Depth (m)	Body Length (cm)	Period (days no.)	Dive-rate Depth (m)
Narwhals						
Melville Bay 1993	3960T	M	5	> 400	245 – 332	> 8 m
Melville Bay 1993	3961T	M	5	> 400	235 – 274	> 8 m
Melville Bay 1993	3962T	M	5	> 450	245 – 277	> 8 m
Melville Bay 1993	6335	F	1	> 400	239 – 281	> 8 m
Melville Bay 1993	20162	M	1	> 400	244 – 284	> 8 m
Melville Bay 1994	20167T	M	5	405	239 – 646	> 8 m
Melville Bay 1994	20688	F	5	310	237 – 334	> 8 m
Melville Bay 1994	20689	F	5	405	238 – 261	> 8 m
Melville Bay 1994	20690	+F	5	> 400	237 – 280	> 8 m
Tremblay Sound 1997	3963T	M	5	375	231 – 237	> 8 m
Tremblay Sound 1997	3964T	M	5	370	233 – 248	> 8 m
Tremblay Sound 1997	6335T	M	5	440	236 – 312	> 8 m
Tremblay Sound 1997	20682	+F	5	400	222 – 254	> 8 m
Tremblay Sound 1997	20691	M	5	306	233 – 252	> 8 m
Tremblay Sound 1998	3960	M	6	> 400	225 – 233	> 12 m
Tremblay Sound 1998	3961	M	6	500	238 – 308	> 12 m
Tremblay Sound 1998	20162	M	5	475	234 – 396	> 8 m
Tremblay Sound 1998	20692	F	5	380	231 – 278	> 8 m
Tremblay Sound 1998	20696	F	5	380	238 – 286	> 8 m
Tremblay Sound 1999	20168T	M	5	444	224 – 294	> 8 m
Tremblay Sound 1999	20687	F	8	390	225 – 297	> 8 m
Tremblay Sound 1999	20688	F	8	415	227 – 311	> 8 m
Tremblay Sound 1999	20689	F	8	405	227 – 355	> 8 m
Tremblay Sound 1999	20690	F	8	400	233 – 239	> 8 m
Tremblay Sound 1999	20691	F	8	350	233 – 279	> 8 m
Belugas						
Devon Island 1995	20688	M	5	465	257 – 294	> 8 m
Devon Island 1995	20689	F	5	404	257 – 304	> 8 m
Devon Island 1995	20690	F	5	368	255 – 292	> 8 m
Devon Island 1995	20694	F	5	372	259 – 304	> 8 m
Devon Island 1995	20695	F	5	392	259 – 311	> 8 m
Devon Island 1995	20696	M	5	408	260 – 323	> 8 m
Devon Island 1996	20683	F	5	354	237 – 308	> 8 m
Devon Island 1996	20684	M	5	400	247 – 308	> 8 m
Devon Island 1996	20685	F	5	370	248 – 294	> 8 m
Devon Island 1996	20686	F	5	412	249 – 318	> 8 m
Devon Island 1996	20687	M	5	423	249 – 305	> 8 m
Devon Island 1996	20688	M	5	487	252 – 326	> 8 m
Devon Island 1996	20689	M	5	454	252 – 254	> 8 m
Devon Island 1996	20690	F	5	400	258 – 301	> 8 m
Devon Island 1996	20693	F	5	405	250 – 297	> 8 m
Somerset Island 1996	17000	F	4/6/10	431	197 –294	> 6 m
Somerset Island 1996	17001	F	4/6/10	415	200 – 273	> 6 m
Somerset Island 1996	17002	F	4/6/10	386	199 – 267	> 6 m
Somerset Island 1996	17003	+F	4/6/10	392	202 – 286	> 6 m
Somerset Island 1996	17004	F	4/6/10	401	199 – 286	> 6 m
Somerset Island 1996	17006	F	4/6/10	396	200 – 305	> 6 m
Somerset Island 1996	17007	M	4/6/10	417	205 – 307	> 6 m
Somerset Island 1996	17008	+F	4/6/10	366	208 – 268	> 6 m
Somerset Island 1996	17009	F	4/6/10	348	204 – 234	> 6 m
Somerset Island 1996	17010	M	4/6/10	457	208 – 338	> 6 m
Somerset Island 1996	17011	M	4/6/10	386	208 – 295	> 6 m
Cumberland Sound 1998	7925	M	5	300	243 – 286	> 8 m
Cumberland Sound 1998	17000	M	5	381	239 – 242	> 8 m
Cumberland Sound 1998	17001	M	5	300	242 – 299	> 8 m
Cumberland Sound 1998	20682	M	5	391	239 – 311	> 8 m
Cumberland Sound 1998	20683	F	5	310	240 – 247	> 8 m
Cumberland Sound 1998	20684	F	5	391	240 – 297	> 8 m
Cumberland Sound 1998	20685	F	5	333	240 – 306	> 8 m
Cumberland Sound 1999	7926	M	6	411	249 – 322	> 8 m
Cumberland Sound 1999	20162	M	8	475	245 – 366	> 8 m
Cumberland Sound 1999	20682	+F	8	356	245 – 326	> 8 m
Cumberland Sound 1999	20683	M	8	419	249 – 365	> 8 m
Cumberland Sound 1999	20684	F	8	338	245 – 340	> 8 m
Cumberland Sound 1999	20685	F	8	427	247 – 344	> 8 m

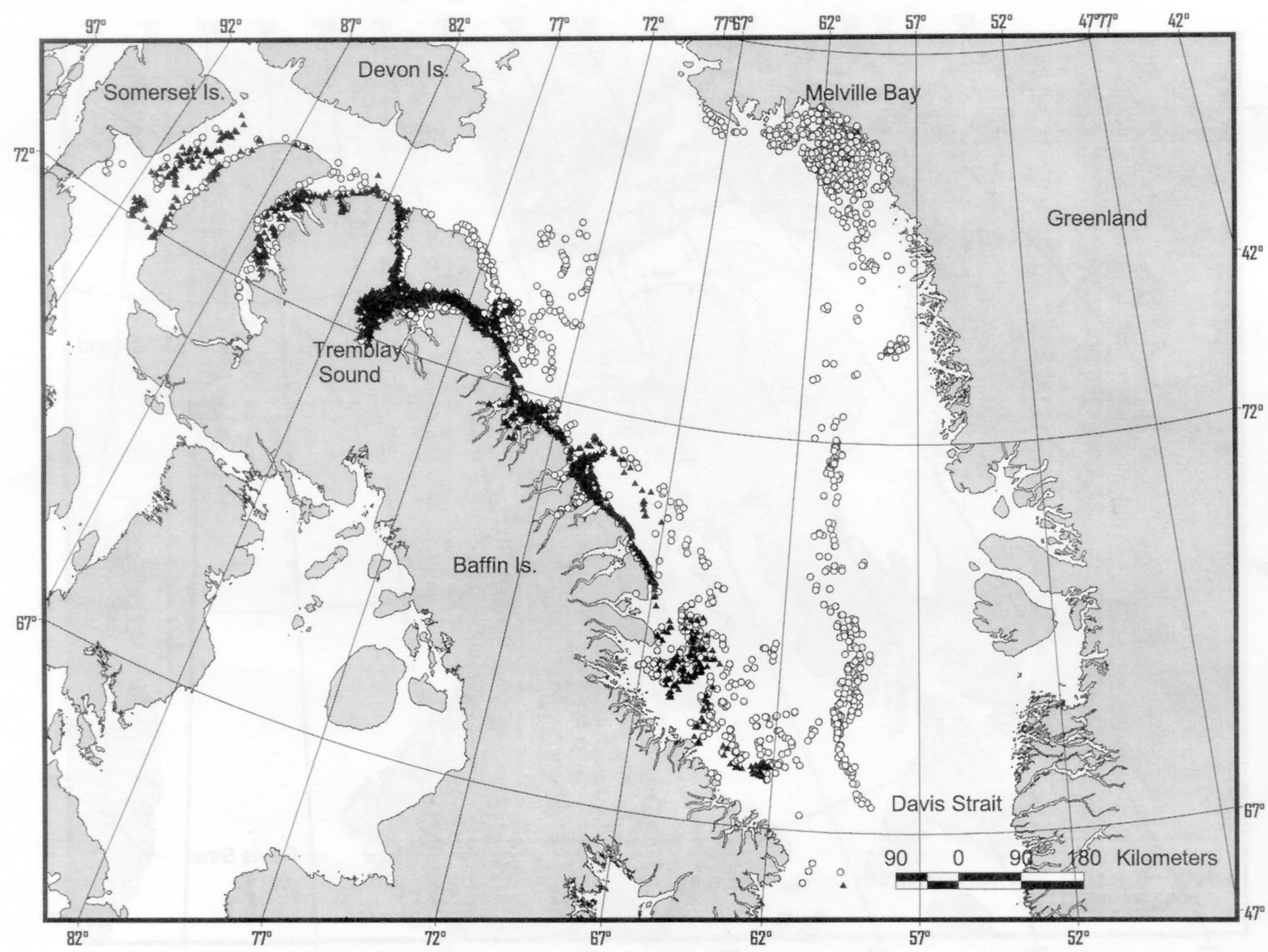

FIG. 1. Positions of narwhals (females = closed triangles; males = open dots) from which data on surfacing time and dive rate were collected.

from coastal to deeper offshore areas. Belugas and female narwhals were instrumented with backpack transmitters, which provided data for shorter periods than the best-performing transmitters, those attached to the tusks of male narwhals. Narwhals were tracked from both the east and west sides of Baffin Bay (Melville Bay in Greenland and Tremblay Sound in Canada, Fig. 1). Nine out of 12 female narwhals stayed in coastal areas until contact was lost, whereas 7 out of 13 males and a few females moved south towards deeper offshore areas in Davis Strait (Dietz and Heide-Jørgensen, 1995; Dietz et al., 2001). Belugas tagged at Somerset Island stayed near the island in shallow estuaries and coastal areas until the eastward movement started in early September (Fig. 2; Richard et al., 1998, 2001). The belugas that were instrumented at Devon Island were moving eastward through Lancaster Sound, passing close along the island's southern coast. When leaving Lancaster Sound, the belugas from Somerset and Devon Islands went north into Jones Sound. All except one of them stayed in the southern part of Smith Sound until contact was lost in late November. Male belugas stayed farther north than females. One beluga, however, crossed Baffin Bay to Greenland and traveled south along the coast towards Disko Bay (Richard et al., 1998, 2001). The belugas that were instrumented in Cumberland Sound stayed in the sound until contact was lost in early January (Richard, Heide-Jørgensen and Orr, unpubl. data).

Effects of Depth Intervals on Beluga Surfacing Times and Dive Rates

Not all transmitters were programmed to use the same depth intervals for data acquisition. It was therefore necessary to elucidate how much of the variation could be attributed to slight alterations of the depth intervals used.

The surfacing times within 0–6 m depth of the 11 belugas from Somerset Island measured in 1996 were significantly longer (ca. 22%) than those of all the other belugas measured within 0–5 m depth during the same period (60.0% vs. 46.4%, days no. 237–323). The surfacing times measured at 0–4 m depth were also longer (ca. 11%) than those measured at 0–5 m, but the difference

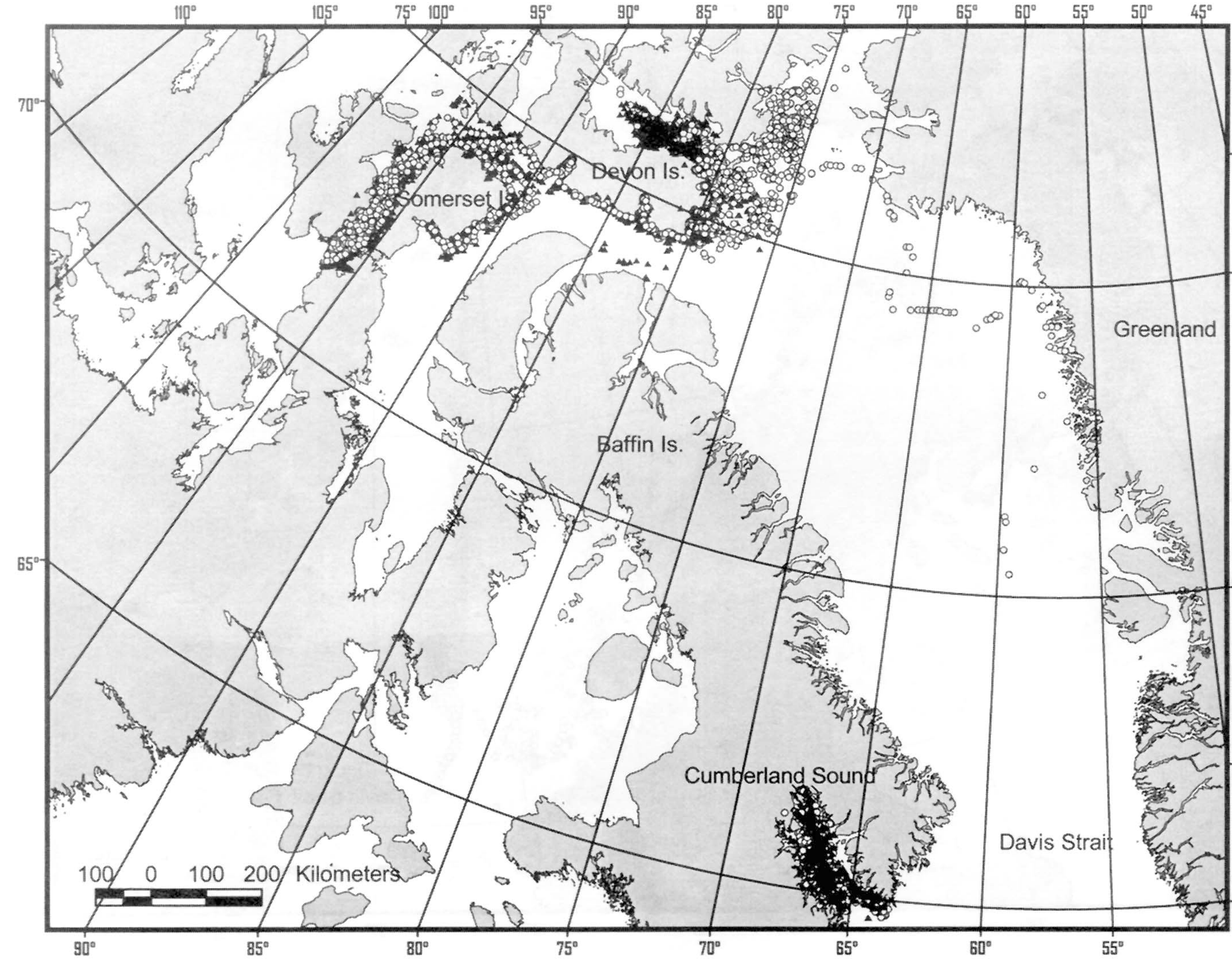

FIG. 2. Positions of belugas (females = closed triangles; males = open dots) from which data on surfacing time and dive rate were collected.

was smaller (51.9% vs. 46.4%). Regression of 0–4 m surfacing times vs. day number had slopes that were parallel to the regressions for 0–5 m surfacing times (ANCOVA with day no. as covariate, $p = 0.72$). Since the 0–4 m surfacing times from the Somerset belugas were closest to the 0–5 m surfacing times from all the other belugas, the 0–4 m interval was used for the comparisons with the other whales.

Dive rates for dives deeper than 6 m for the belugas from Somerset Island were significantly higher ($p < 0.0001$) than dive rates for dives deeper than 8 m for all the other belugas during the same period (days no. 238–325). The difference was too large (ca. 2 dives/h) to be ignored.

Surfacing Times for Narwhals and Belugas

Data on surfacing times for belugas and narwhals were acquired over different but overlapping periods, so comparison of surfacing times was restricted to periods with data from both species (days no. 222–396) and with comparable depth intervals (0–4 and 0–5 m). For data measured in comparable ways, narwhals spent significantly less time at the surface (mean = 42.1%, n = 1537) than belugas (mean = 49.8%, n = 5423, $p < 0.0001$, ANOVA, Fig. 5). Narwhals at Melville Bay and Tremblay Sound did not differ in surfacing times, but the three beluga localities (Devon Island, Somerset Island, and Cumberland Sound) differed significantly (days no. 222–336). The lowest mean surfacing times were found among the whales from Devon Island (44.9%) and Cumberland Sound (51.6%), and the highest, among those from Somerset Island (53.8%). Therefore, more detailed analyses of temporal changes in behaviour and differences related to age and sex classes were needed to describe the variability.

Effects of Body Length, Sex, and Presence or Absence of a Calf on Surfacing Time

Whales of different sex and size classes were instrumented, and we expected physiology-related parameters (e.g., surfacing times) to vary accordingly. However,

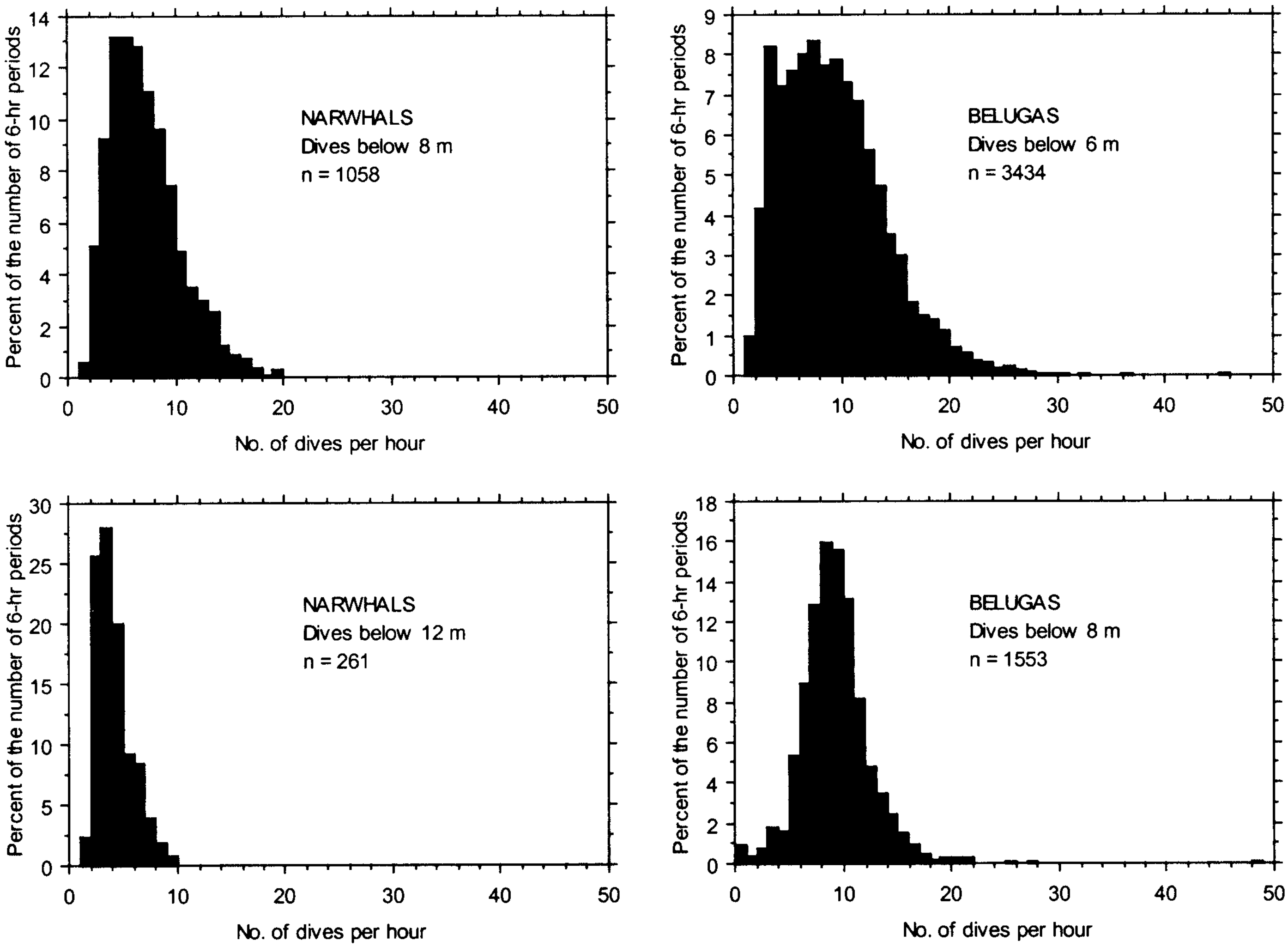

FIG. 3. Frequency distribution of dive rates (number of dives per hour) for narwhals and belugas measured during 6 h periods.

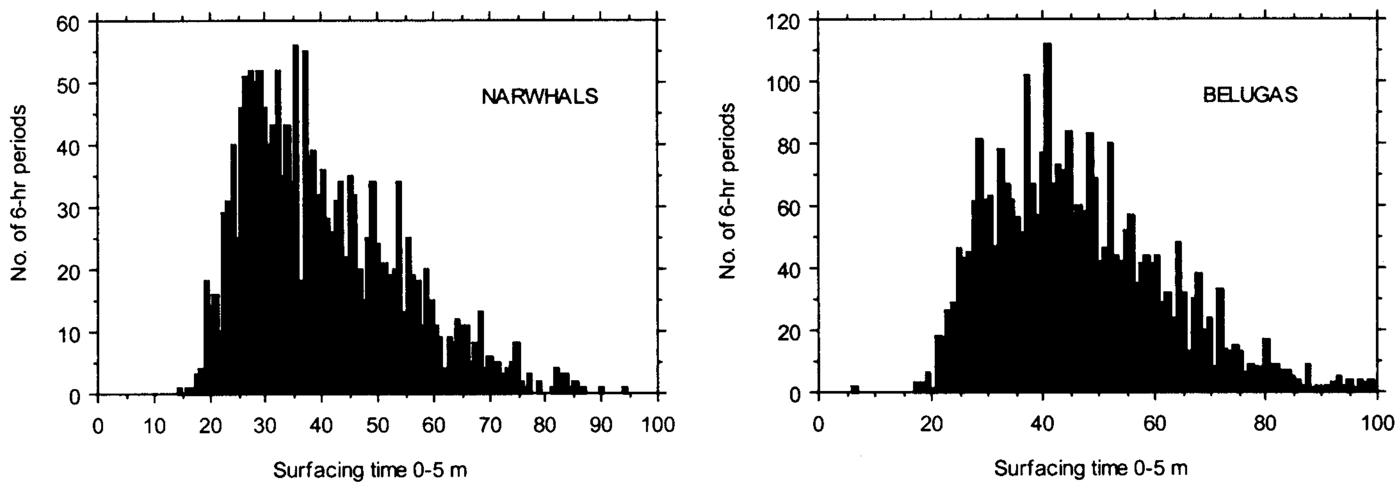

FIG. 4. Frequency distribution of surfacing times for narwhals (n = 1740 6 h periods with measurements) and belugas (n = 2982) measured in the depth interval 0–5 m.

the main descriptor of size—standard body length—was not measured consistently for all whales (Table 1). Even when correctly measured, body length does not necessarily give a linear prediction of a whale's volume or mass.

For belugas, surfacing times declined with increasing body length as determined by four length classes (300–350 cm, 350–400 cm, 400–450 cm, > 450 cm; Table 2). No pattern was obvious for narwhals. Female belugas with

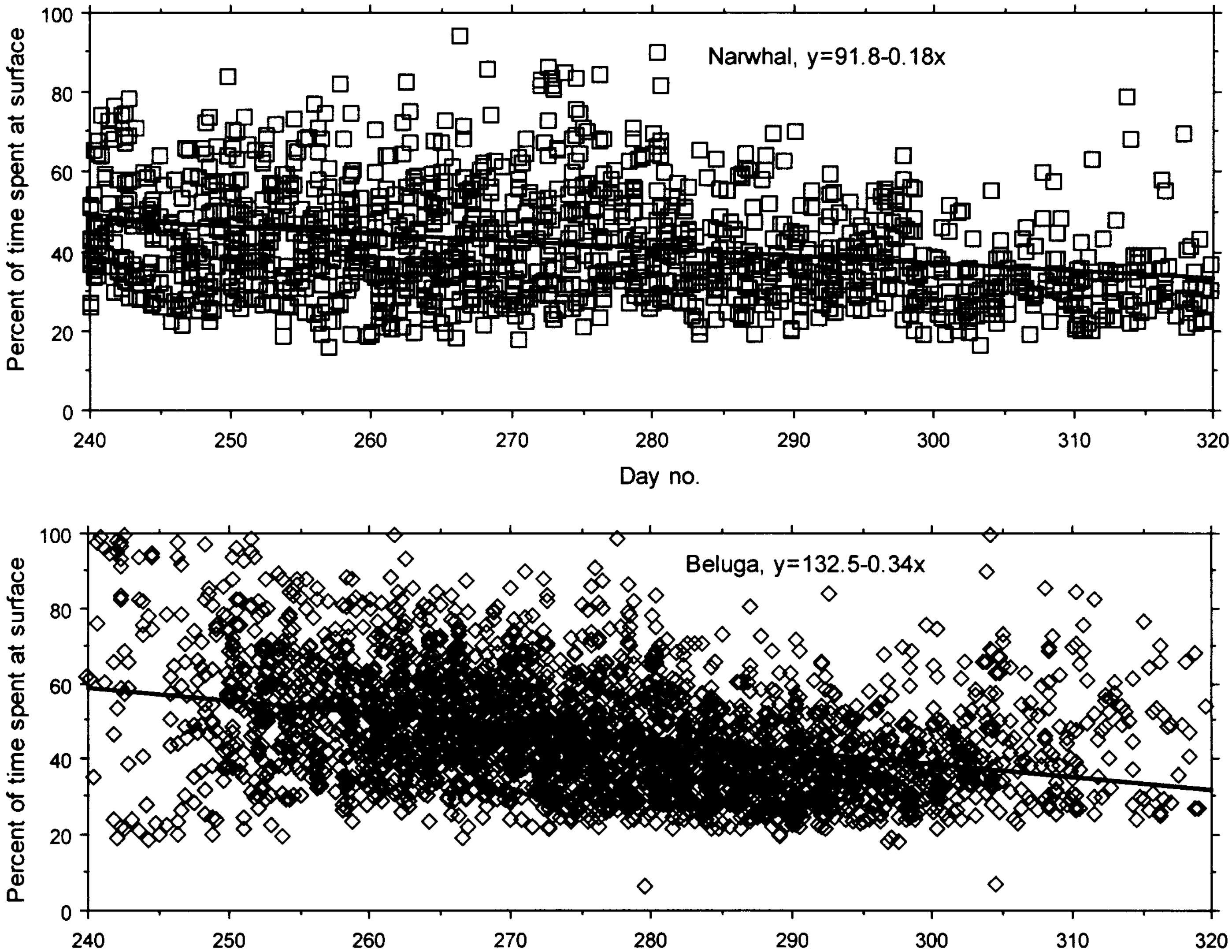

FIG. 5. Surfacing times for narwhals and belugas for the period with data for both species measured in the depth interval 0–5 m.

calves spent more time at the surface (0–6 m) than did females without calves (64% vs. 59%, $p < 0.001$). This was evident also for the surface defined as 0–4 m but not for the 0–10 m interval. Again, no similar effect could be detected for narwhals. Female narwhals surfaced for similar periods regardless of whether they had calves. They also had significantly longer surfacing times than male narwhals, but this trend was not evident for belugas (ANCOVA with day no. as covariate, Table 2).

Fine-scale Surfacing Time for Belugas

For the belugas from Somerset Island, the surfacing times could be split into four categories between 0 and 6 m. The whales spent up to 100% of their time at the surface (0–6 m) from the day of their instrumentation (days no. 197–207) to day 211 (29 July). This is a period when the whales congregate in shallow estuaries and do not dive. To distinguish offshore from estuarine surfacing times, those values greater than 90% were excluded from the sum of 0–6 m depth categories. The following analysis refers only to the surfacing times when the whales supposedly were offshore.

On average, the whales spent 5% of each 6 h period at 0 m (see Table 3). This percentage increased slightly ($\beta = 0.014$, $p = 0.0002$) with increasing total surfacing time (0–6 m). However, it must be kept in mind that the surfacing times were calculated over six hours. As some proportion of the 6 h periods may have been spent in estuaries, the estimates may be biased towards longer surfacing times. This 'noise' caused by estuarine visits, which we cannot eliminate completely, may explain the unexpected rise in 0 m surfacing time with increasing total surfacing time.

Taken as a percentage of the total surfacing time (0–6 m), the 0 m category decreased significantly with increasing total surfacing time ($\beta = -0.161$, $p < 0.0001$). This

TABLE 2. Surfacing times (0–5 m) and dive rates (> 8 m) of narwhals and belugas by sex, size class, and months. Standard deviations are given in parentheses.

Species	Sex	% Mean Surfacing Time	Mean Dive Rate in Dives/h
Narwhal	female	48.5 (14.4)	6.4 (2.9)
Narwhal	male	38.1 (11.9)	8.7 (3.6)
Narwhal	both	41.1 (13.6)	7.9 (3.6)
Beluga	female	45.0 (15.1)	8.3 (3.2)
Beluga	male	48.4 (15.2)	8.7 (2.9)
Beluga	both	46.5 (15.2)	8.5 (3.0)
	Size		
Narwhal	< 375 cm	41.5 (15.4)	8.9 (2.4)
Narwhal	375 – 424 cm	52.3 (15.0)	5.6 (2.4)
Narwhal	425 – 474 cm	39.9 (12.2)	8.3 (3.9)
Narwhal	≥ 475 cm	38.0 (12.9)	7.8 (2.7)
Beluga	< 350 cm	50.3 (14.4)	9.1 (2.5)
Beluga	350 – 399 cm	46.0 (14.9)	8.1 (3.3)
Beluga	400 – 449 cm	45.6 (16.1)	8.8 (3.2)
Beluga	≥ 450 cm	46.7 (13.8)	8.1 (2.6)
	Month		
Narwhal	1	26.7 (3.0)	7.1 (2.3)
Narwhal	2	25.8	7.1 (2.4)
Narwhal	5	34.0 (6.2)	
Narwhal	8	46.3 (13.0)	7.4 (3.9)
Narwhal	9	44.9 (14.3)	8.6 (3.9)
Narwhal	10	40.3 (12.0)	7.7 (3.6)
Narwhal	11	32.7 (8.8)	7.2 (2.4)
Narwhal	12	29.6 (6.3)	7.8 (2.3)
Beluga	1		8.1 (2.2)
Beluga	8	67.8 (25.7)	8.3 (4.9)
Beluga	9	51.7 (14.9)	8.8 (3.2)
Beluga	10	40.9 (12.6)	8.3 (2.8)
Beluga	11	44.6 (15.3)	8.2 (3.4)
Beluga	12		8.6 (2.1)

decrease was countered by significant increases in both the 0–2 m and 2–4 m depth categories ($\beta = 0.056$ and $\beta = 0.114$). The 4–6 m category decreased with increasing total surfacing time ($\beta = -0.009$) but not significantly ($p = 0.201$).

The relative proportions among the four depth categories were on average 10.3% (SD = 6.1) at 0 m, 69.3% (SD = 10.0) at 0–2 m, 11.7% (SD = 6.1) at 2–4 m, and 8.7% (SD = 5.9) at 4–6 m.

The total surfacing time was apparently unrelated to sex, body size, or period of the day. After day number 237 (24 August), all 10 belugas from Somerset Island that were still transmitting showed a significant decline in percentage of time spent at the surface (0–6 m), from 0.02 to 0.70 percentage points per day (0.34 on average). By far the greatest reduction in surfacing time was in the 0–2 m category, where the average decline was 0.30 percentage points per day. Only the 0 m category increased slightly (0.03 percentage points/day).

Fine-scale Surfacing Time for Narwhals

Two narwhal tags from Melville Bay in 1993 measured the surface as any depth less than 1 m, and two from Tremblay Sound in 1998 measured it as any depth less than 6 m; the rest used 5 m as the surface threshold (Table 1).

TABLE 3. Surfacing times in nine depth intervals for belugas inside the estuaries (selected for more than 89% of time within 6 m of the surface) and outside them (selected for less than 90% of time within 6 m of the surface).

	Inside the Estuaries		Outside the Estuaries	
Interval	Mean %	SD	Mean %	SD
Surface				
0 m	13.3	22.4	5.4	3.2
0 – 2 m	72.8	21.0	39.0	13.2
2 – 4 m	7.5	6.7	6.8	4.6
4 – 6 m	2.8	3.4	4.8	3.6
Sum: 0 – 6 m	96.4	3.5	56.0	15.8
6 – 8 m	1.3	1.5	4.0	3.7
8 – 10 m	0.6	0.8	2.9	2.9
10 – 20 m	0.8	1.1	8.1	8.6
> 20	< 1	–	28.9	–

For the period with data for all three surfacing thresholds (days no. 241–281), the means were 22.0% (SD = 8.4) for 0–1 m, 45.6% (SD = 14.2) for 0–5 m, and 64.0% (SD = 19.5) for 0–6 m. However, the slopes of the regressions of the three different measures of surface time vs. day number varied significantly. Thus no overall proportion for all the surfacing thresholds can be given.

Diurnal Differences in Surfacing Times and Dive Rates

The possible influence of time of day on surfacing times or dive rates was evaluated by comparing data acquired during four 6 h periods of each day.

Surfacing time was independent of time of day within 0–5 m depth for any one locality and both species. This was also true when surfacing times of more than 90% (inshore behaviour) were analyzed separately for the belugas from Somerset Island at 0–4, 0–6, or 0–10 m (Table 4). The Cumberland Sound belugas spent less time within 0–8 m during the night than during the day.

There were no diurnal differences in dive rates for narwhals from Melville Bay (deeper than 8 m) or Tremblay Sound (deeper than 8 and 12 m). The mean dive rate for dives deeper than 8 m was significantly higher for narwhals from Melville Bay (8.6/h) than for the Tremblay Sound whales (7.2/h). Similarly, no effects of time of day on dive rates were discernible for belugas from Somerset Island (in or outside estuaries) or from Devon Island in 1995. However, for Devon Island whales in 1996, time of day had a significant effect (ANCOVA) on the dive rate: more dives occurred in the evening (1700–2300 h), and the dive rate declined steadily toward the afternoon (Table 5). In Cumberland Sound, there was a trend toward more night dives and fewer afternoon dives in both 1998 and 1999.

Temporal Changes in Surfacing Times

Surfacing times of narwhals were measured from August through June, but only sporadically after January (Fig. 6). In general, surfacing times declined steadily from

TABLE 4. Distribution of average (SD in parentheses) surfacing times for belugas from three localities and years. The sampling periods monitored are shown for each locality. The whales from Cumberland Sound monitored in 1999 showed a significant effect of sampling period on surfacing time ($_{***}$ indicate $p < 0.0001$).

Localities and Year	6 h Periods			
	1700 – 2300	2300 – 0500	0500 – 1100	1100 – 1700
Devon Island 1995; 0 – 5 m	38.7 (11.2)	38.0 (10.1)	38.9 (12.4)	41.1 (12.9)
	2100 – 0300	0300 – 0900	0900 – 1500	1500 – 2100
Devon Island 1996; 0 – 5 m	48.1 (15.1)	47.9 (14.7)	47.8 (15.0)	49.2 (15.4)
Somerset Island 1996; 0 – 4 m	51.5 (15.9)	52.5 (16.3)	53.6 (15.7)	52.6 (15.8)
Somerset Island 1996; 0 – 6 m	54.9 (15.8)	55.7 (15.7)	57.5 (15.5)	56.6 (15.9)
Somerset Island 1996; 0 – 10 m	57.6 (17.0)	58.0 (16.8)	60.3 (16.7)	59.6 (16.2)
Cumberland Sound 1998; 0 – 5 m	48.6 (12.5)	53.2 (14.0)	56.0 (16.5)	51.4 (15.7)
Cumberland Sound 1999; 0 – 8 m ***	37.3 (11.2)	58.4 (16.9)	56.8 (15.7)	46.7 (14.9)

TABLE 5. Distribution of average (SD in parentheses) dive rates for belugas from three localities and years. The sampling periods monitored are shown for each locality. The whales from Devon Island in 1996 and Cumberland Sound 1999 showed a significant effect of sampling period on dive rates ($_{***}$ indicate $p < 0.0001$).

Localities and Year	6 h Periods			
	1700 – 2300	2300 – 0500	0500 – 1100	1100 – 1700
Devon Island 1995	7.2 (2.4)	8.4 (3.6)	7.5 (2.9)	7.2 (2.6)
	2100 – 0300	0300 – 0900	0900 – 1500	1500 – 2100
Devon Island 1996 ***	8.8 (3.3)	8.0 (2.9)	7.7 (2.7)	7.6 (2.6)
Somerset Island 1996	8.8 (4.5)	8.9 (4.2)	8.7 (4.4)	8.6 (4.3)
Cumberland Sound 1998	9.1 (3.1)	8.7 (2.9)	8.5 (3.1)	8.7 (2.9)
Cumberland Sound 1999 ***	10.5 (3.2)	9.0 (2.9)	8.7 (3.2)	9.1 (2.3)

August through early November and then remained steady around 30% (Table 2). The surfacing time for one narwhal (#20696) that was tracked for an adequate period (50 days) showed a slight increase (β = 0.99) in surfacing time (0–5 m) in autumn. One of the two narwhals for which surfacing time was measured at 0–6 m reduced its surfacing time significantly during the autumn, whereas the other individual was tracked for too short a time. The few data points for narwhals from November through February indicate that surfacing time remained low (25–33% of each 6 h period) during this period (Table 2).

For belugas, data on surfacing time (0–5 m) were collected from mid-July through early January (Fig. 7). There was no trend for the period from July to late August. From 1 September, the surfacing times declined significantly for belugas from all three localities (Somerset Island, Devon Island, and Cumberland Sound) and without significant differences between the localities. All belugas showed a decline in surfacing time at 0–5 m, and for Somerset Island the decline was evident in all three depth measurements.

The 0–8 m surfacing time measured in Cumberland Sound in 1999 showed a much larger proportion (10 percentage points) of time spent at surface than was shown in 1998, when the surface time was measured at 0–6 m.

For the period with data from both narwhals and belugas (days no. 241–329), i.e., late August through late November) and comparable surface definitions (0–4 and 0–5 m), the belugas (β = -0.31) showed a faster reduction in surfacing time than the narwhals (β = -0.17).

Relationship between Surfacing Time and Dive Rate

The effect of increasing number of dives (dive rate) on the time spent at the surface was evaluated by regressing the surfacing time on the dive rate, both measured in 6 h intervals, where the significance of the effect was determined by ANOVA.

For belugas, the surfacing times declined within the 0–2 m, 0–4 m, 0–5 m, and 0–6 m depth intervals, with increasing dive rates below depths of 6 m and 8 m (Table 6). Measurements of surfacing time at a depth of 0 m, which represent the periods when the transmitter was dry, also declined with increasing number of dives. Further stratification of the 'surface' in intervals between 2–4 m and 4–6 m showed an increase in surfacing time with increasing dive rate, with the largest increase in the 4–6 m interval. Measurements of surfacing time in the 0–10 m interval showed that surfacing time increased significantly with increasing dive rate for belugas from Somerset Island; however, the opposite trend was found among belugas from Cumberland Sound in 1999, when surfacing time was measured in the 0–8 m interval.

For narwhals, no effect on surfacing times (0–5 m) with increasing dive rates (> 8 m) could be observed (Table 6). When the surfacing depth interval was increased to 0–6 m

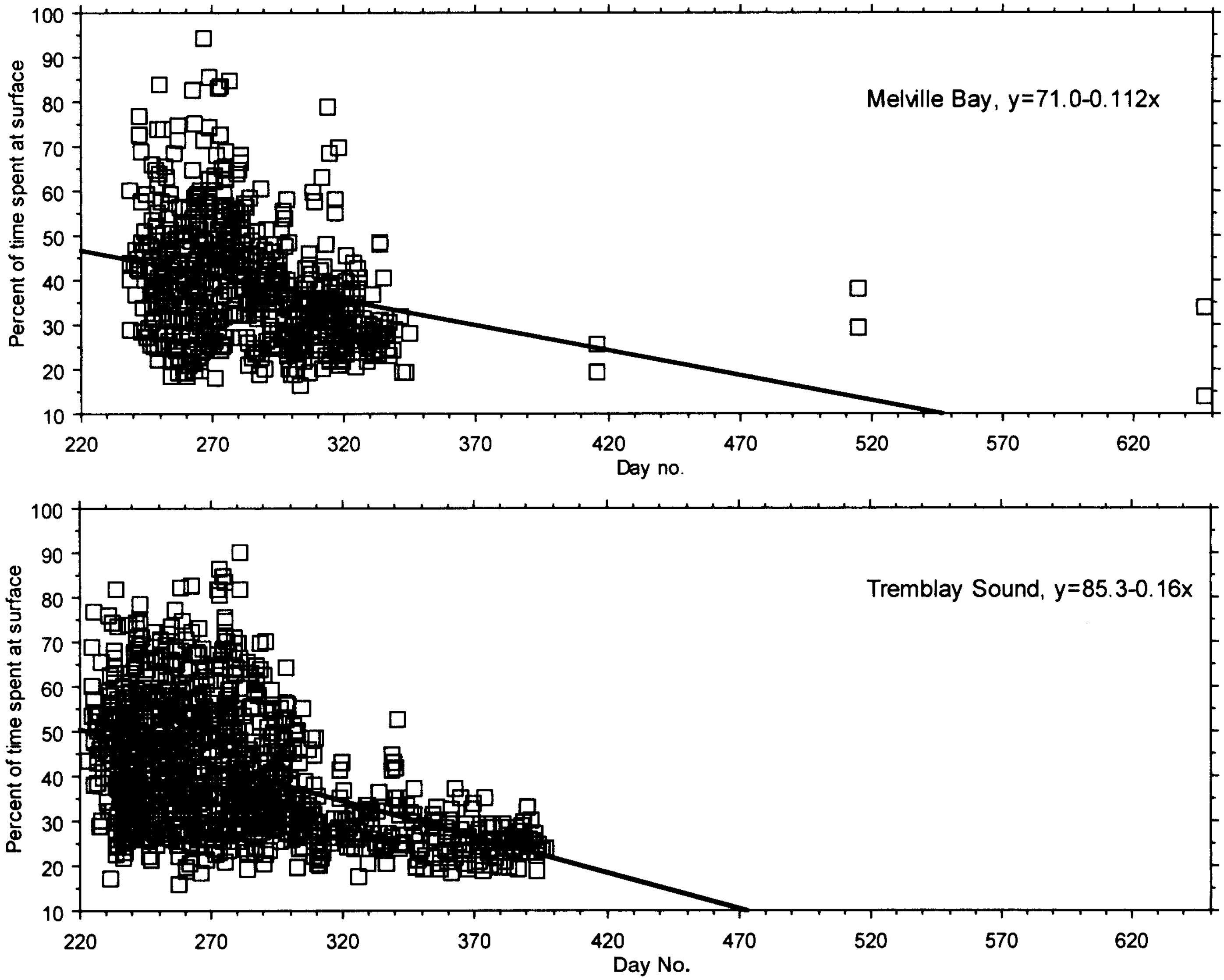

FIG. 6. Changes in surfacing times (0–5 m depth interval) for narwhals from Melville Bay and Tremblay Sound.

and the dives deeper than 12 m were included, an insignificant decline in surfacing time with increasing dive rate was observed.

Belugas that between day 197 and day 211 (29 July) spent at least part of a 6 h sampling period in an estuary were defined as those with high surfacing times (≥ 90% at 0–6 m, see above). Dive rates for the 6 h periods in which the whales presumably spent time in estuaries (mean = 5.8 dives/h, 95% CI: 5.1–6.5) were significantly lower (t-test) than the dive rates for 6 h periods with lower surfacing times (< 90%, mean = 8.7 dives/h, 95% CI: 8.3–9.1). Evidently, when the whales are in shallow and perhaps turbid water, they make relatively few dives deeper than 6 m.

Comparison of Dive Rates for Narwhals and Belugas

Dive rates ranged from a minimum of 1 dive/h (depths > 8 m) to about 20 dives/h for both species. Narwhals made significantly fewer dives/h (mean = 7.5, SD = 3.4) than belugas (8.6, SD = 3.7) for the period with comparable data (days no. 222–366) and depth thresholds (dives > 8 m).

Female narwhals from Melville Bay had significantly higher dive rates (9.0 dives/h) than female narwhals from Tremblay Sound (6.0 dives/h) when rates were averaged over periods with comparable data (days no. 235–334), but the difference was not significant for males (9.0 vs. 8.4 dives/h). When narwhals from both localities were combined, males had significantly higher dive rates than females (Table 2).

Similarly, the belugas of both sexes from Devon Island had a significantly lower dive rate than those from Cumberland Sound for comparable periods.

Seasonal Changes in Dive Rates

Seasonal changes in dive rates can be assessed on the basis of the mean number of dives accumulated over 24 h, or the longest period available, to avoid possible diurnal

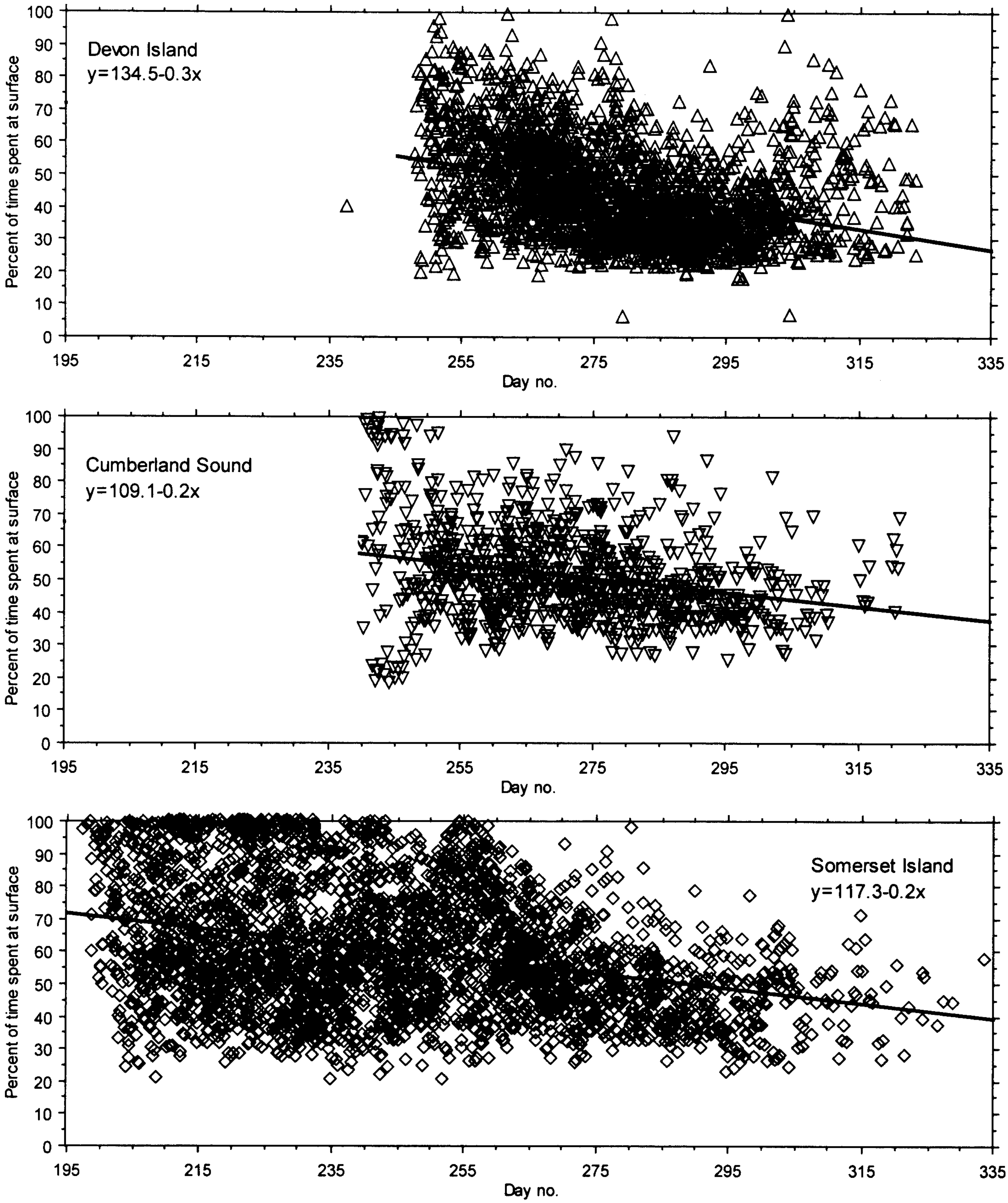

FIG. 7. Changes in surfacing times for belugas from Cumberland Sound (0–5 m depth interval), Devon Island (0–5 m), and Somerset Island (0–4 m).

TABLE 6. The relationship between the surfacing time (percentage of time spent at the surface in certain depth intervals) and the dive rate (number of dives per hour below certain depth thresholds) for belugas and narwhals, both measured during 6 h periods from whales tagged in different areas. The effect is evaluated by regression of surfacing time on dive rate, and the significance of the effect is measured by ANOVA.

Species/Tagging Area	Surfacing Interval	Dive Rate Measured Below	Number of 6 h Periods with Measurements	Coefficient of Regression	Significance of Effect
Belugas					
Cumberland Sound and Devon Island	0 – 5 m	8 m	2823	-0.231	0.0097
Somerset Island	0 m	6 m	3010	-0.081	< 0.0001
Somerset Island	0 – 2 m	6 m	3010	-0.945	< 0.0001
Somerset Island	2 – 4 m	6 m	3010	+0.331	< 0.0001
Somerset Island	4 – 6 m	6 m	3010	+0.470	< 0.0001
Somerset Island	0 – 4 m	6 m	3010	-0.696	< 0.0001
Somerset Island	0 – 6 m	6 m	3010	-0.226	0.0012
Somerset Island	0 – 10 m	6 m	2312	0.827*	< 0.0001
Cumberland Sound	0 – 8 m	8 m	674	-0.72	0.0069
Narwhals					
Melville Bay and Tremblay Sound	0 – 5 m	8 m	1541	0.132	0.1721
Tremblay Sound	0 – 6 m	12 m	184	-1.478	0.0528

* The interval where surfacing time is measured (0–10 m) goes deeper than the depth below which the dive rate is measured (6 m).

effects (Fig. 8). For the period with comparable data (days no. 241 – 329, i.e., late August through late November) there was a significant decline ($p < 0.0001$) in dive rate (deeper than 8 m) for belugas ($\beta = -0.013$), but not for narwhals ($\beta = -0.007$). This trend, however, was not evident for the dive rates of whales if the number of dives was enumerated as those deeper than 6 m for belugas ($\beta = 0.007$, $p = 0.4531$) or 12 m for narwhals ($\beta = 0.329$, $p = 0.0527$), again restricted to the same autumn period. Apparently the number of dives deeper than a certain threshold depth (6 m) does not change seasonally for belugas, whereas the dive rate measured as dives deeper than 8 m does. The lack of a significant trend for the 12 m depth threshold can be attributed to the low sample size (1 narwhal with a total of only 70 dive rate measurements).

Whales from Somerset Island, Devon Island, and Melville Bay showed a significant decline in dive rate. The steepest declines were observed in the whales from Devon Island ($\beta = -0.033$, $p < 0.0001$) and Melville Bay ($\beta = -0.031$, $p < 0.0001$), which were also the whales that moved the longest distances. The belugas from Cumberland Sound did not change their dive rate ($\beta = -0.002$, $p = 0.6$), and the narwhals from Tremblay Sound increased their dive rate ($\beta = 0.016$, $p = 0.018$).

Evaluated on an individual basis, the one narwhal with adequate data on dive rate at 12 m increased its dive rate during the autumn. Of 16 narwhals with data on dives greater than 8 m, 3 increased their dive rate and 4 decreased it during the autumn. Of 25 belugas with dive rates measured as dives deeper than 8 m, 4 increased their dive rate during the autumn, 8 decreased it, and 12 did not change the dive rate. Seven out of 11 belugas from Somerset Island increased their rate of dives greater than 6 m during the autumn; three decreased their rate of dives; and one maintained a constant dive rate.

For Devon Island, the beluga dive rate decreased in both 1995 and 1996, and the means increased significantly from 1995 to 1996. In Cumberland Sound, the dive rate increased in 1998 and decreased in 1999, and the difference in means was also significant for the period with comparable data. Narwhals in Tremblay Sound increased their dive rates in 1997 and 1999, but not in 1998; the 1997 mean was significantly higher than those for the two later years, which did not differ. Narwhals in Melville Bay decreased their dive rate in 1993, but not in 1994; the mean dive rate was significantly lower in 1994.

Effects of Body Length, Sex, and Offspring on Dive Rates

Female belugas reduced their dive rate during the autumn faster than the males ($\beta = -0.01$ vs. $\beta = -0.006$ for dives deeper than 8 m, ANCOVA, $F = 8.92$, $p = 0.0029$). Generally, larger whales made fewer dives than smaller whales, and the differences in means were significant for all comparisons except the size classes of 350–400 cm and 400–450 cm (Table 2). The smallest whales (< 350 cm), however, increased their dive rate significantly during the autumn in contrast to the three larger size groups (ANOVA, $F = 14.03$, $p = 0.0001$).

The belugas from Cumberland Sound had a significantly higher mean dive rate than those from Devon Island (9.1/h vs. 7.9/h; dives > 8 m; days no. 237 – 326). The difference was especially evident for the Cumberland Sound males (diff. 1.5/h vs. 1.1/h), but male belugas in all three areas had significantly higher dive rates (0.7/h) than females.

The difference in dive rates (deeper than 8 m) among narwhals for the two sexes attained constant proportions over time, with about 1.7 more dives per hour for males (mean = 8.2/h, SD = 2.8) compared to females (mean = 6.4/h, SD = 3.5, ANCOVA). No consistent patterns of the effects of body size on dive rate (> 8 m) could be detected among narwhals, probably because the number of tagged

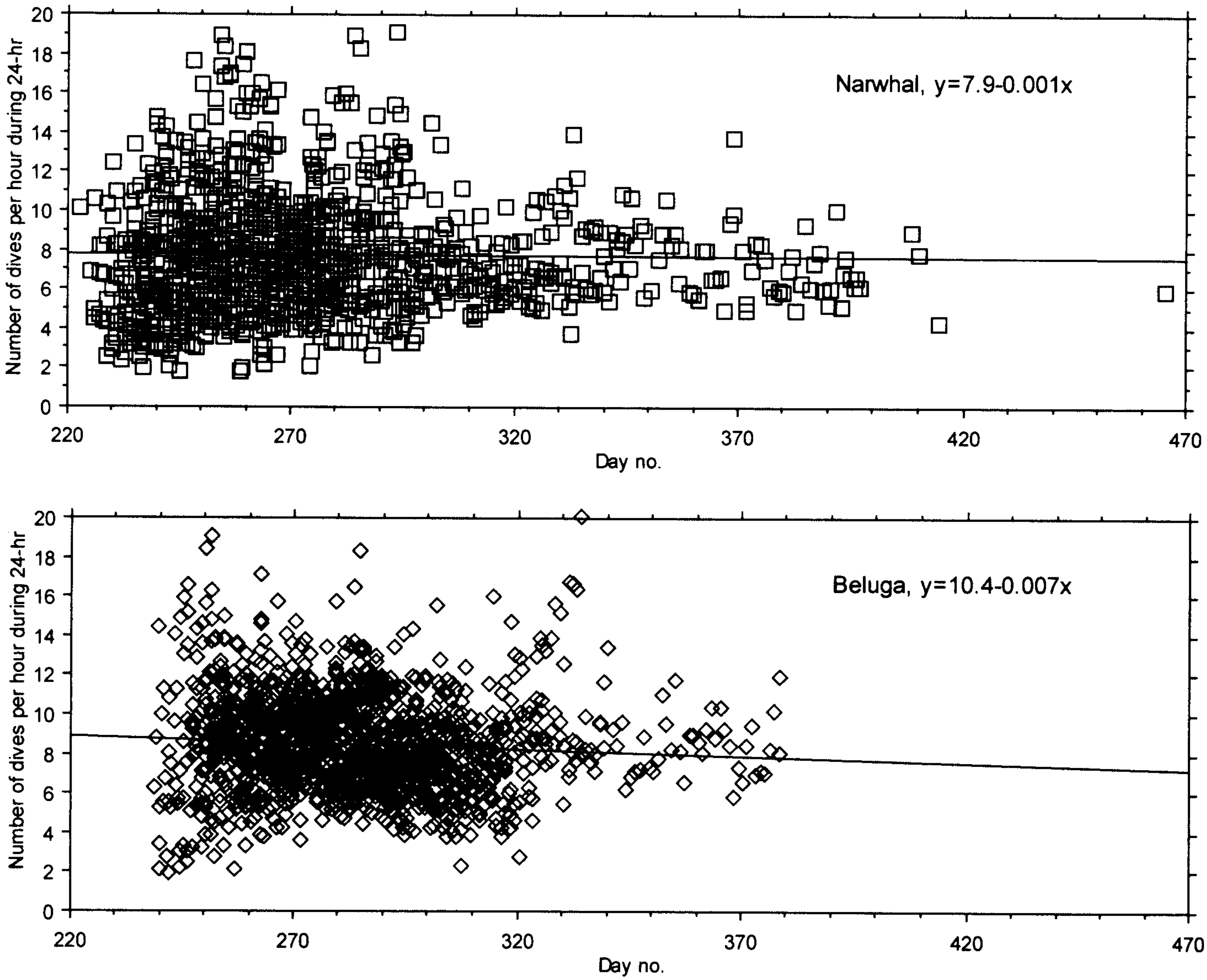

FIG. 8. Seasonal changes in dive rates below 8 m for narwhals and belugas assessed on a 24 h basis.

whales was smaller and proper length measurements were missing for several of the whales.

Female narwhals accompanied by calves had slightly but not significantly lower dive rates (> 8 m) than females without calves. However, this difference was significant for belugas from Somerset Island (> 6 m, ANCOVA with day as covariate).

DISCUSSION

Our decision to omit outliers from the analysis seems somehow inadequate, as it does not allow for detection of errors within the range of the data that we considered plausible. Also, the 2% truncation of the outliers is an arbitrary setting, and the possible range of the data may be still smaller. However, the fact that the analyses are based on a fairly large amount of data will likely minimize any effects of erroneous data, whether at the extremes or within the range considered plausible.

There seems to be a consistent asymptotic lower level of surfacing time in the depth interval 0–5 m at around 20% for both belugas and narwhals. Few surfacing times were less than 20%. Because of their rare occurrence, they are considered to be in error. Apparently both species need to spend at least 20% of their time within the 0–5 m depth for physiological reasons. The only comparable data available come from satellite tracking of one narwhal in Tremblay Sound in 1993, and that animal spent 55.7% of its time at or within 5 m of the surface during August (Martin et al., 1994). The average for eight whales that we tracked in the same area and season was 46.7%.

Belugas that visited estuaries in July spend most, if not all, of their time at or close to the surface, as also observed by Martin and Smith (1992). It is therefore reasonable to exclude the data for periods when the whales were in estuaries from analyses of diving behaviour in offshore areas. Whales were suspected to have been in estuaries when surfacing times were very large (> 90%). The basic sampling period was 6 h, and the whales could spend a variable proportion of the 6 h period in an estuary. No strict criteria were applied to discriminate estuarine surfacing times. Thus the 'greater than 90% criterion' identifies only the extreme occasions when almost all of the time was spent in an estuary. This problem particularly confounds the analysis of surfacing times in July and the first half of August.

Evidently the whales spend a declining percentage of their time at the surface from August through October, a trend that is independent of species, area, sex, or size. The longest surfacing times occurred in the summer, when the whales congregated in coastal areas. Belugas that visited shallow estuaries spent particularly large proportions of their time at the surface.

Narwhals seem to spend shorter periods at the surface than belugas, a fact evidently related to their more offshore distribution and deeper diving behaviour. In contrast to belugas, narwhals do not spend much time in estuaries or other shallow areas, though they may spend substantial time near the surface milling and socially interacting in summer (e.g., Pilleri, 1983).

The decline in surfacing times of both species in autumn may be related to the whales' offshore movements toward wintering habitats. The decline starts when the whales leave the coastal habitats, and the timing varies between localities, presumably depending on the formation of fast ice. For example, belugas from Somerset Island start moving offshore earlier in the autumn than the belugas from Cumberland Sound, where ice-free water persists longer. Similarly, narwhals from Melville Bay leave their coastal habitats later than the narwhals from Tremblay Sound (Dietz et al., 2001). Pack ice up to several meters thick may prevail at some of the wintering grounds, and this may cause the whales to make shorter visits to the surface just for breathing and not for resting. When leaving the summering grounds, the whales also start to feed more intensively (see Davis and Finley, 1979; Finley and Gibb, 1982; Welch et al., 1993), and this must also influence their surfacing times, as both narwhals and belugas takes prey items near or on the bottom (Finley and Gibb, 1982; Heide-Jørgensen and Teilmann, 1994; Heide-Jørgensen et al., 1994). Travelling to new areas usually takes place at the surface, however, and the autumn surfacing times are likely composed partly of periods during which the whales are travelling.

Dive rates show a consistent range of values for species, sex, and length classes, but the relation to time of the year is more equivocal than for the surfacing times. Apparently some whales increase their dive rate during autumn, while most of them reduce their dive activity. It probably depends on availability of food resources in different areas. Future analyses of dive rate should incorporate both the actual depth of the dives and the spatial distribution of the whales. Another factor that influences the dive rate is the horizontal movement of the whales. Thus, the sedentary belugas from Cumberland Sound exhibited greater diving activity than the whales from Somerset Island, Devon Island, and Melville Bay that moved to offshore areas in the autumn. Apparently the whales choose between spending the movements on vertical or horizontal activity.

The data presented here can potentially be used to 'correct' or compensate for one of the negative biases in density and abundance estimates from visual and photographic aerial surveys of belugas and narwhals. The assumption of the constant sightability of whales down to 5 m depth may need to be justified by further studies. It certainly depends on the clarity of the water masses being surveyed. Shallow waters with silt-laden river runoff have much lower transparency than the offshore areas frequented by the whales in winter. This study shows the possible range and variability of the values for surfacing times and the likely range of these in seasons that remain to be sampled. It is somehow surprising that the variability is so limited and that the surfacing times seem relatively robust. Nevertheless, the application of specific values to correct for whales that were submerged and therefore invisible during a survey will depend on species, season, and area, and no general conversion factor can be recommended at this stage.

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