Diving behaviour of narwhals (*Monodon monoceros*) at two coastal localities in the Canadian High Arctic

Kristin L. Laidre, Mads Peter Heide-Jørgensen, and Rune Dietz

Abstract: In August 1999 and 2000, four suction-cup-attached time–depth recorders (TDRs) were deployed and retrieved from narwhals (*Monodon monoceros*) in Tremblay Sound, Baffin Island, and Creswell Bay, Somerset Island, Nunavut, Canada. The TDRs remained on the whales for between 12 and 33 h and collected 64.5 h of dive data. Mean dive depths ranged from 20.8 m (SD = 14.8 m) to 50.8 m (SD = 43.8 m) and mean dive durations ranged from 3.4 min (SD = 1.6 min) to 4.9 min (SD = 4.5 min). There appeared to be individual differences in dive parameters both within a region and between regions. Three of the whales made short, shallow dives, while another whale made dives twice as deep and twice as long. One whale had maximum dive durations (>20 min) that exceeded predicted aerobic dive limits for narwhals. There was a strong relationship between maximum dive depth and duration for all whales ($p < 0.0001$). Narwhals spent between 30.3 and 52.9% of their time at depths <5 m and the range of correction factors for availability bias was 1.9–3.3. Satellite-linked TDRs were simultaneously deployed on the whales at both localities. Dive data collected using the two methods were compared and good agreement between the methods was obtained.

Résumé : En août 1999 et 2000, quatre chronobathymètres enregistreurs (TDRs) à ventouses ont été installés puis récupérés chez des narvals (*Monodon monoceros*) dans le détroit de Tremblay de l’île de Baffin et dans la baie de Creswell de l’île Somerset, Nunavut, Canada. Les appareils sont restés fixés aux narvals de 12 à 33 h et ont accumulé 64,5 h de données sur la plongée. La profondeur moyenne des plongées se situait entre 20,8 m (écart type = 14,8 m) et 50,8 m (écart type = 43,8 m) et leur durée moyenne, entre 3,4 min (écart type = 1,6 min) et 4,9 min (écart type = 4,5 min). Il semblait y avoir des différences individuelles dans les paramètres de plongée, au sein d’une région et d’une région à l’autre. Trois des narvals faisaient des plongées courtes et peu profondes, alors qu’un autre effectuait des plongées deux fois plus profondes et deux fois plus longues. Un narval faisait des plongées dont la durée maximale (>20 min) excédait la durée maximale théorique de plongée aérobie chez le narval. Il y avait une forte corrélation entre la profondeur maximale et la durée des plongées chez tous les narvals ($p < 0,0001$). Les narvals passaient de 30,3 à 52,9 % de leur temps à des profondeurs <5 m et l’étendue des facteurs de correction du biais de disponibilité était de 1,9 à 3,3. Des TDRs reliés à un satellite ont été utilisés en même temps sur les narvals des deux sites et la comparaison des données recueillies par les deux méthodes a révélé une bonne concordance des résultats.

[Traduit par la Rédaction]

Introduction

The narwhal (*Monodon monoceros*) is a High Arctic ice-associated cetacean that travels thousands of kilometres each year between shallow coastal summering grounds and deep offshore wintering grounds. From July through September, narwhals visit inshore bays and fjords in the Canadian High Arctic Archipelago and Greenland. The populations of narwhals that summer in these sheltered waters move south in September to spend the winter months in areas covered by dense offshore pack ice in Baffin Bay and Davis Strait. The diving behaviour of narwhals has been studied by means of both visual observations from coastal promontories on their summering grounds (Silverman 1979; Dueck 1989) and satellite tagging operations (Martin et al. 1994; Heide-Jørgensen and Dietz 1995; Dietz et al. 2001; Heide-Jørgensen et al. 2001). Narwhals are thought to make relatively shallow dives on their summering grounds, and increase their dive depths on the wintering grounds, where they feed on Greenland halibut (*Reinhardtius hippoglossoides*), polar cod (*Boreogadus saida*), Arctic cod (*Arctogadus glacialis*), and squid species (*Gonatus* spp.) (Vibe 1950; Finley and Gibb 1982; Heide-Jørgensen et al. 1994). Narwhals are among the deepest diving cetaceans and have been documented to reach depths

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of 1000–1500 m (Heide-Jørgensen and Dietz 1995; Heide-Jørgensen et al. 2001, 2002).

All of the information on narwhal diving behaviour collected during tagging operations has been from whales instrumented with satellite-linked time–depth recorders (SLTDRs) (Martin et al. 1994; Dietz and Heide-Jørgensen 1995; Heide-Jørgensen and Dietz 1995; Heide-Jørgensen et al. 2001). SLTDRs, the instruments most widely used to study cetacean diving behaviour, collect both an animal's geographic position and information on dive data. SLTDRs may organize data into a series of depth bins over discrete time intervals or transmit limited amounts of data on diving behaviour just prior to satellite reception. SLTDRs can record large amounts of data and do not need to be recovered from the animal for data retrieval. However, because of constraints imposed by the satellite system (e.g., amount of data, band width, and limited surfacing time of the whales) and battery life, the data collected from these instruments are summarized and compressed, or only fractions of the data are ever transmitted and received by the satellite. This imposes limitations on data analysis and interpretation.

Time–depth recorders (TDRs) are instruments that sample depth (as well as velocity, light level, and temperature) every 1–5 s and record data in an uncompressed format. Detailed information on dive profiles, destination depths, and ascent and descent rates can be obtained from TDRs, and data collected from these instruments can be used to corroborate dive data collected using other methods. One limitation of TDRs is that the tag must be retrieved from the animal on which it was deployed in order to obtain the data stored in the memory. Because of this feature, TDRs are generally deployed on marine mammals when there is a good chance that the tag will be recovered (i.e., the animal returns to a breeding colony or haulout site). This technique lends itself well for use with pinnipeds with predictable movements. For cetaceans, which tend to be wide-ranging and elusive, TDRs can be retrieved when the instrument (generally attached with suction cups) falls off the whale. In this case, the risk of losing the instrument increases, and as a consequence, TDRs have been successfully deployed in few studies of cetaceans. As a result, TDR data collected from cetaceans tend to be short in duration (hours or days) and high resolution.

Both SLTDRs and TDRs are becoming an integral part of studies of the diving behaviour of marine mammals as tag size decreases and attachment time is improved. Four suction-cup-attached TDRs were deployed and retrieved from free-ranging narwhals in Tremblay Sound, Baffin Island, and Creswell Bay, Somerset Island, Nunavut, Canada, in August 1999 and 2000. We present the detailed diving data obtained from the narwhals, which are among the few TDR data collected from cetaceans, and the first ever at this resolution from this species. At the same time, SLTDRs were deployed simultaneously on the whales, providing an opportunity to compare fragments of data from these two types of tags.

Materials and methods

Narwhals were live-captured from the beach in Tremblay Sound (72.3°N, 81.1°W) in August 1999 and in Creswell Bay (72.7°N, 94.2°W) in August 2000 (Fig. 1), using nets set perpendicular from the shore. Tremblay Sound, located on the east side of the Borden Peninsula of Baffin Island, is a long (45 km), narrow (2–7 km wide) fjord. Creswell Bay, located on the east side of Somerset Island (approximately 50 km long and 40 km wide), opens into Prince Regent Inlet. Whales were handled in the nets immediately after they were captured and belts were placed around the midsection, tail, head, and tusk for restraint. Whales were positioned between two inflatable boats offshore and both SLTDRs and TDRs were attached. SLTDRs (Wildlife Computers, Redmond, Wash.) were attached to the female whales on the dorsal ridge and to the tusk of males using two stainless-steel bands. The dorsal-ridge transmitters were attached to the whales with two 8 mm long polyethylene pins secured with nylon washers and nuts. Research was conducted in accordance with principles and guidelines of the Canadian Council on Animal Care. See Dietz et al. (2001) for additional details of SLTDR tag design, attachment, and performance.

The TDRs (Mk7, Wildlife Computers, Redmond, Wash.) were attached to a flotation device consisting of three oval net buoys held together with 6 mm long nylon pins made to withstand pressure at over 400 m. A cylindrical hole drilled in the center of the three buoys contained a VHF transmitter (154 MHz) with an antenna perpendicular to the surface of the water. The TDR was anchored by a lead weight to improve stability. The antenna position provided both successful VHF tracking of the instrumented animal and successful retrieval when the instrument fell off and washed ashore. The TDR and buoys were mounted on the back of the whale behind the blowhole with two suction cups, positioned approximately 10 cm ahead of the buoys and 15 cm apart (Fig. 2). All tags had a depth range of 0–1000 m.

The whales were tracked from promontories along the coast with VHF receivers immediately after they were released. Once a constant signal was received, tags were located and retrieved by an inflatable boat. If 24 h had passed and no signal was received, a helicopter search was initiated to retrieve the instrument. When the tags were recovered, the data were downloaded into a PC for analysis. Drift in the depth values was corrected using the software Zero-Offset Correction version 1.27 (Wildlife Computers), and data were processed using Dive Analysis (Wildlife Computers) to produce summary statistics for each dive. The minimum depth to be considered a dive was set at 8 m for TDR data. All dives below this depth were analyzed in “Dive Analysis”. The TDR sampled pressure (depth), velocity, light level, and temperature every second. From these variables, dive depth, dive duration, ascent and descent rates, and proportional time at depth were calculated.

The SLTDR tags transmitted the number of dives in each of 14 depth and 10 duration bins for each of four 6-h periods of the day. The proportion of time spent at the surface, mean dive depth, and mean dive duration were calculated from the SLTDR data for each complete sampling period and from the TDR data during the same temporal periods. Only 6-h periods with both complete SLTDR datasets and complete TDR sampling were compared. Results were compared for three individuals. The TDR data were analyzed with respect to SLTDR programming, where depth to be considered a “dive” and depth to be considered the “surface” varied by

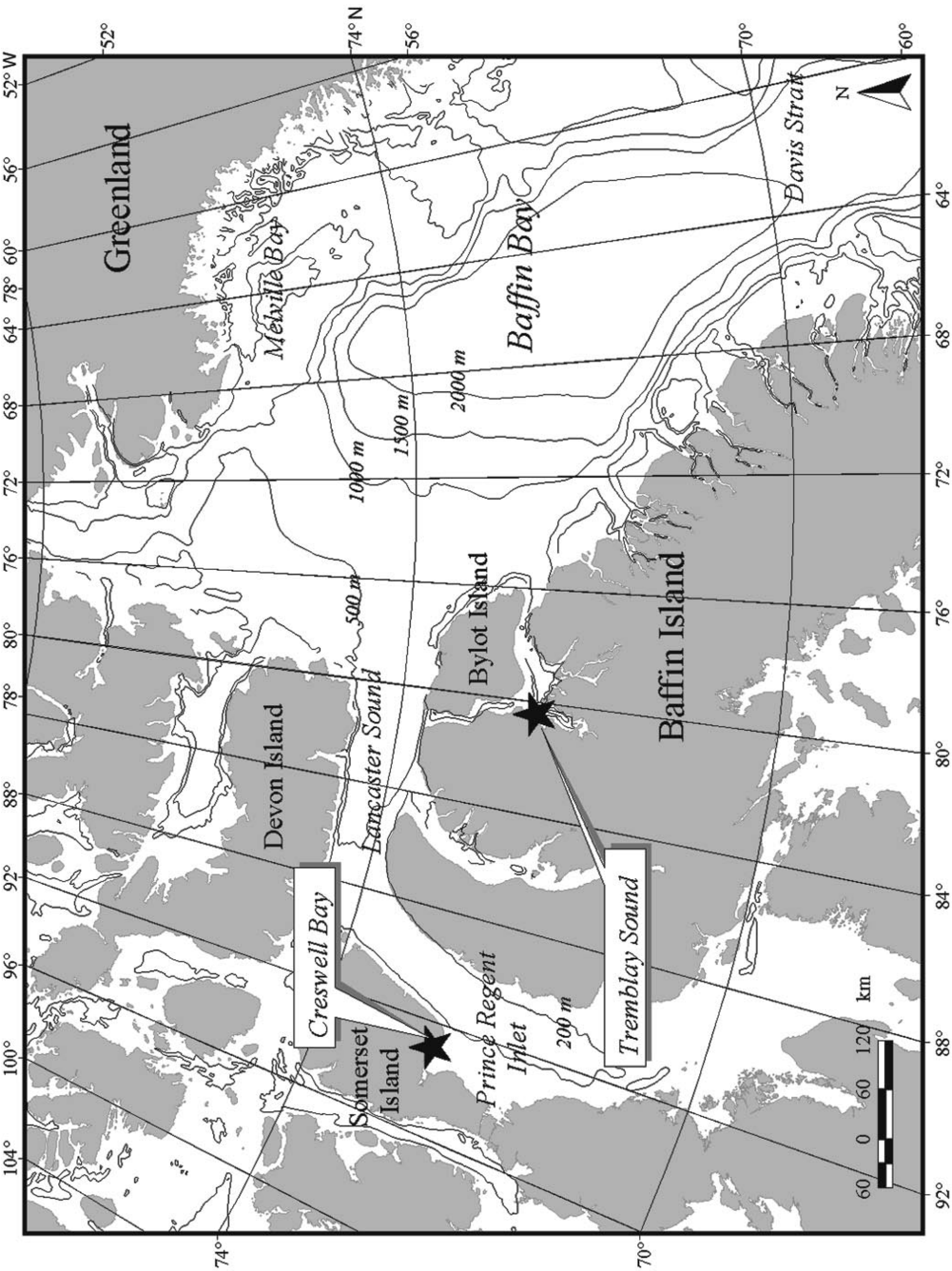
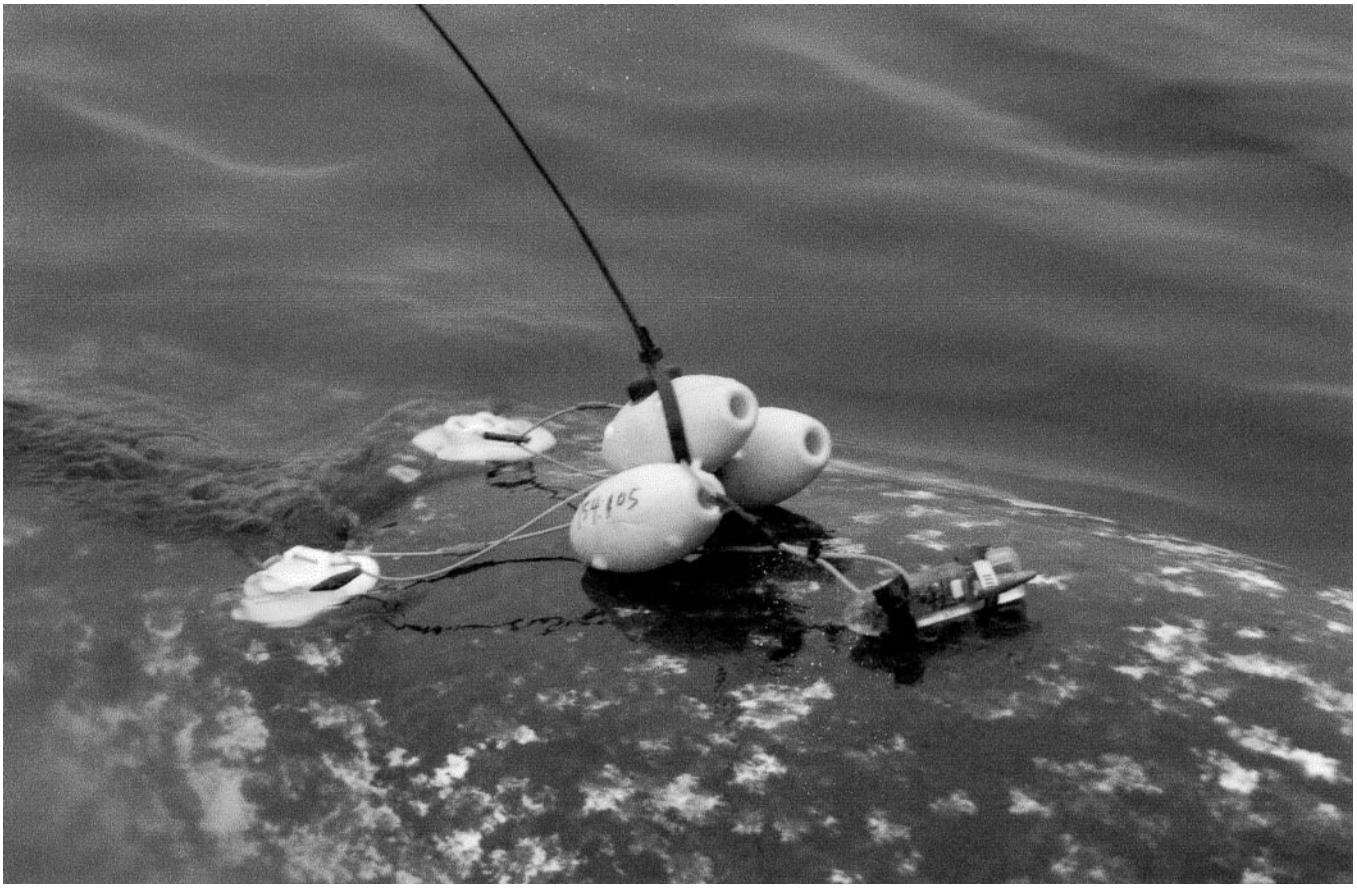


Fig. 1. Locations of tagging sites and place names mentioned in the text. Bathymetric contours are shown on the map.

Fig. 2. Image of suction-cup-attached time–depth recorder (TDR) on a narwhal (*Monodon monoceros*) in Creswell Bay, August 2000. Note the round buoys attached to the suction cup with wire. The TDR is attached underneath the buoy cluster and rests on the narwhal's back.



individual. Mean dive depths for the SLTDR data were calculated using the midpoint of each depth bin using the following formula:

$$\text{meandepth}_i = \sum_{j=1}^{14} \text{middepth}_j(\text{dives}_{ij}/\text{totaldives}_i)$$

where meandepth_i is the average dive depth for period i, middepth_j is the middle value of the depth category j, dives_{ij} is the number of dives in depth category j for period i, and totaldives_i is the total number of dives in period i. Mean dive durations for the SLTDR data were calculated using the following formula:

$$\text{meanduration}_i = \sum_{j=1}^{10} \text{midduration}_j(\text{dives}_{ij}/\text{totaldives}_i)$$

where meanduration_i is the average dive duration for period i, midduration_j is the middle value of duration category j in period i, dives_{ij} is the number of dives in duration category j for period i, and totaldives_i is the total number of dives in period i. The level of significance was 0.05 for all t tests, regressions, analyses of variance (ANOVAs), and post-hoc analyses.

Results

Tremblay Sound

Approximately 25.5 h of dive data were collected from whales tagged in Tremblay Sound in 1999. Three TDRs were deployed on narwhals, two of which were successfully retrieved and downloaded. The first tag was deployed on an adult male (MM-1) with a body length of 410 cm and tusk length of 118 cm. The tag was deployed on 12 August 1999 at approximately 00:15 and was successfully retrieved 4 days later on 16 August 1999 at approximately 12:51. The TDR on MM-1 collected data for 13 h. The second successful data recovery was from a tag deployed on an adult male (MM-2) with a body length of 444 cm and tusk length of 178 cm. The tag was deployed on 21 August 1999 at approximately 07:30 and was successfully retrieved on 22 August 1999 at approximately 19:30. The TDR on MM-2 collected data for 12.5 h.

After release, both whales dove immediately, spending no time at the surface. MM-1 immediately made a 124 m deep dive lasting 14 min, and MM-2 immediately dove to approximately 120 m (12 min duration) after release. Both whales equipped with TDRs stayed in Tremblay Sound throughout the recording period.

Creswell Bay

Approximately 39 h of dive data were collected from narwhals tagged in Creswell Bay in 2000. Three TDRs were deployed on whales, two of which were successfully retrieved and downloaded. The first successful tag recovery was from an adult female (MM-3) with a body length of 390 cm and tail width of 95 cm. The tag was deployed on 14 August 2000 at 08:20:00 and was successfully retrieved on 19 August 2000 at 17:00. The TDR on MM-3 collected data on the whale for approximately 6 h. The second tag was deployed on an adult female narwhal (MM-4) with a body length of 370 cm and tail width of 100 cm. The tag was deployed on 14 August 2000 at approximately 07:30:00 and was successfully retrieved on 25 August 2000 at 12:10. The tag collected 33 h of data. The third tag was observed on the whale approximately 24 h after it was deployed, and VHF surfacing signals were received at this time; however, the tag was never recovered. After the tags were deployed, MM-3 made a series of 20–40 m deep dives for approximately 1 h. MM-4 reacted in a similar way, making dives to depths of 30–40 m for over 1.5 h.

Dive profile and dive rate

In Tremblay Sound, MM-1 made regular deep dives between 100 and 200 m and stayed at the surface for long periods (Fig. 3*a*). The average depth of dives for this individual was 50.8 m (SD = 43.8 m; *n* = 100) (Table 1). The number of dives per hour ranged from 1 to 13, with an average of 7.1 dives/h (SD = 3.2 dives/h) below 8 m. In contrast, MM-2 made multiple shallow dives with shorter surfacing periods, and only reached depths below 100 m three times (Fig. 3*b*). The average depth of dives for this individual was 23.0 m (SD = 28.4 m; *n* = 125). The number of dives per hour below 8 m ranged from 9 to 13, with an average of 10.9 dives/h (SD = 1.2 dives/h) below 8 m. The deepest recorded sounding in Tremblay Sound is approximately 270 m (National Ocean Service, National Oceanic and Atmospheric Administration (NOAA), U.S. Department of Commerce (USDOC)) and maximum depths for both individuals were 256–258 m. Therefore, it appeared that the whales were diving to the bottom of their habitat during the period when they were tracked.

The dive profiles for the two narwhals tagged in Creswell Bay (MM-3 and MM-4) are similar (Figs. 3*c* and 3*d*). Both whales made multiple short, shallow dives over the course of the tracking period. The average depth of dives was 20.8 m (SD = 14.8 m; *n* = 36) for MM-3 and 34.4 m (SD = 16.1 m; *n* = 277) for MM-4 (Table 1). The number of dives per hour for MM-3 ranged from 3 to 9, with an average of 6.0 dives/h (SD = 2.2 dives/h), whereas the number of dives per hour for MM-4 ranged from 3 to 14, with an average of 8.3 dives/h (SD = 2.6 dives/h) (Table 1). The deepest recorded sounding in Creswell Bay is approximately 80 m (National Ocean Service, NOAA, USDOC) and maximum dive depths were 73–75 m, again indicating that the whales dove to the bottom of their habitat.

A typical dive profile for all four whales included a steep descent, a short period at the bottom, a slower ascent, and a slow approach to the surface (Fig. 4). Less typical dives included a stepwise descent, perhaps following the bottom topography, with short periods at the bottom and a steep ascent. Dives with stepwise descent and ascent rates and variation in depth at the bottom were rare. Most dives could be

Table 1. Summary of dive statistics for narwhals (*Monodon monoceros*) tagged in Tremblay Sound, Baffin Island, and Creswell Bay, Somerset Island, Nunavut, Canada.

Narwhal ID	Location	Sex	Body length / tusk length (cm)	Dive depth (m)	Max. depth (m)	Total no. of dives <8 m	No. of dives/h	Dive duration (min)	Max. dive duration (min)	Surfacing interval (min)	Descent rate (m/s)	Ascent rate (m/s)
MM-1	Tremblay Sound	M	410/118	50.8 (43.8)	256	100	7.1 (3.2)	4.9 (4.5)	26.2	3.1 (4.3)	1.3 (0.8)	1.5 (1.6)
MM-2	Tremblay Sound	M	444/178	23.0 (28.4)	258	125	10.9 (1.2)	2.6 (1.7)	11.5	3.2 (3.2)	0.8 (0.4)	0.7 (0.4)
MM-3	Creswell Bay	F	390	20.8 (14.8)	73	36	6.0 (2.2)	3.4 (1.6)	7.0	6.9 (6.6)	0.6 (0.4)	0.6 (0.4)
MM-4	Creswell Bay	F	370	34.4 (16.1)	75	277	8.3 (2.6)	4.3 (1.7)	9.4	2.9 (3.3)	0.6 (0.3)	0.8 (0.3)

Note: The mean and SD (in parentheses) are reported for each category.

Fig. 3. Dive profiles for MM-1 (*a*), MM-2 (*b*), MM-3 (*c*), and MM-4 (*d*). Only a 6-h portion of the dive profile from each individual is shown.

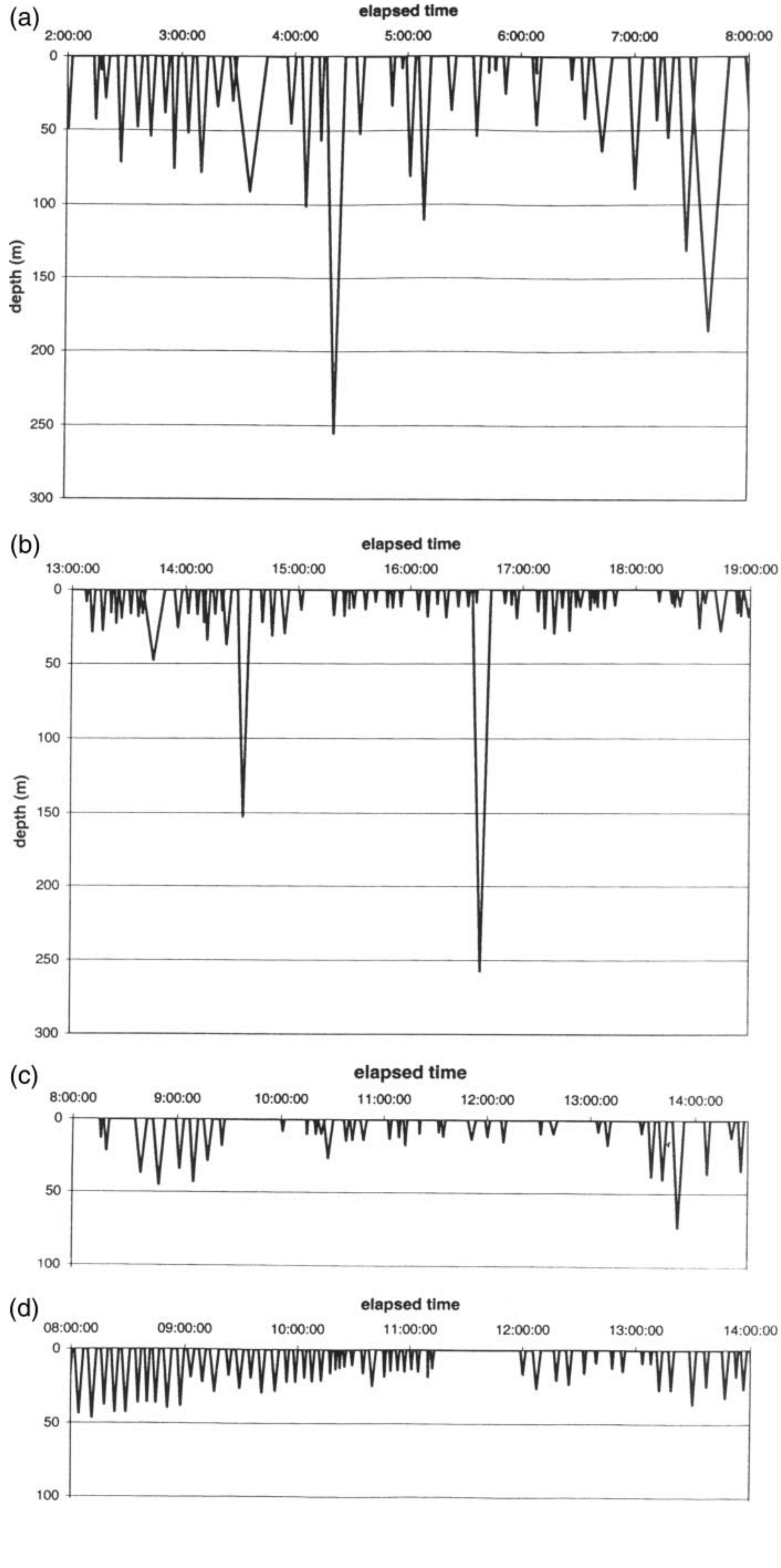
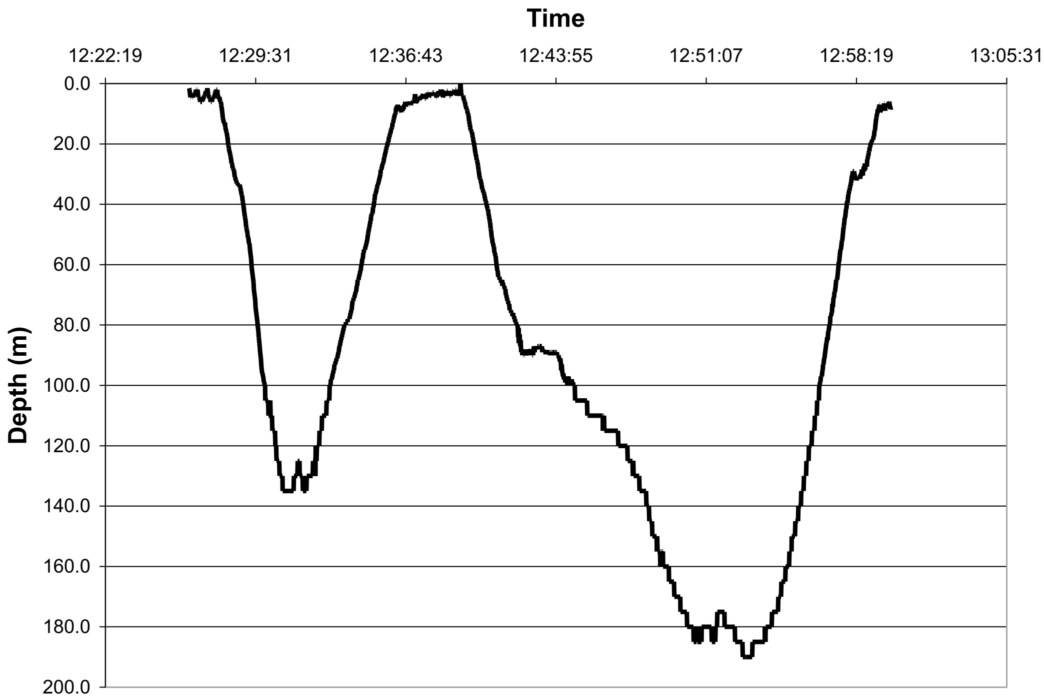


Fig. 4. Representative dive profile taken from MM-1. Note the V-shaped dive and limited bottom time.



classified as V-shaped, with slightly more bottom time than that reported for a V-shaped dive in Martin et al. (1994).

Dive duration and surfacing time

The mean dive durations for MM-1 and MM-2 were 4.9 min (SD = 4.5 min) and 2.6 min (SD = 1.7 min), respectively. The maximum dive duration for MM-1 was 26.2 min, whereas the maximum dive duration for MM-2 was 11.5 min (Table 1). Using all dives, there was a strong significant relationship between the maximum depth of a dive and the duration of that dive (MM-1: $r = 0.783$, $p < 0.0001$; MM-2: $r = 0.7310$, $p < 0.0001$).

The two whales had similar mean surfacing time (where the surface was defined as 8 m depth). The mean surfacing durations for MM-1 and MM-2 were 3.1 min (SD = 4.3 min) and 3.2 min (SD = 3.2 min), respectively (Table 1). The most frequent surfacing duration for MM-1 was between 0 and 1 min ($n = 21$) and the most frequent surfacing duration for MM-2 was between 1 and 2 min ($n = 35$). Eighty-two percent of the surfacing durations were <5 min for MM-1 and 87% were <5 min for MM-2. One long surfacing duration for MM-1 (32 min) occurred just after the first deep dive and two of the long surfacing durations for MM-2 (22 min) occurred right after release (the other occurred approximately 11 h into the tracking period). This second long surfacing duration for MM-2 did not seem to be related to bouts of deep diving because it occurred in the middle of a series of shallow (13–25 m) dives. Post-dive surface time was significantly correlated with dive depth for MM-1 ($r = 0.295$, $0.002 < p < 0.0005$); however, surface time was not significantly correlated with dive depth for MM-2 ($r = 0.141$, $0.1 < p < 0.2$). Post-dive surfacing time was significantly correlated with dive duration for both MM-1 ($r = 0.233$, $p = 0.02$) and MM-2 ($r = 0.213$, $0.02 < p < 0.05$).

The mean dive durations for MM-3 and MM-4 were 3.4 min (SD = 1.6 min) and 4.3 min (SD = 1.7 min), respectively. The maximum dive duration was 7.0 min for MM-3 and 9.4 min for MM-4 (Table 1). Using all dives, there was a strong relationship between the maximum depth of a dive and the duration of that dive (MM-3: $r = 0.741$, $p < 0.0001$; MM-4: $r = 0.815$, $p < 0.0001$).

The mean surfacing durations for MM-3 and MM-4 were 6.9 min (SD = 6.6 min) and 2.9 min (SD = 3.3 min), respectively. The most frequent surfacing duration for MM-3 was between 3 and 4 min, whereas the most frequent surfacing duration for MM-4 was between 2 and 3 min. Ninety-one percent of the surfacing durations were ≤5 min for MM-4, whereas only 60% were ≤5 min for MM-3. The longer surfacing times for MM-3 did not seem to be correlated with bouts of deep diving because they most often occurred between several shallower dives (8–20 m). Post-dive surfacing time was not significantly correlated with dive depth (MM-3: $r = 0.28$, $p > 0.1$; MM-4: $r = 0.022$, $p > 0.5$), nor was it significantly correlated with dive duration (MM-3: $r = 0.234$, $p > 0.1$, MM-4: 0.039, $p > 0.5$).

Ascent and descent rates

Velocity data from MM-1, MM-2, and MM-3 were high for the first dive after the tag was deployed. However, the same velocity was observed later during normal behaviour for all three whales. Mean descent rate was strongly correlated with destination depth for MM-2 and MM-4 (MM-2: $r = 0.666$, $p < 0.001$; MM-4: $r = 0.275$, $p < 0.001$), slightly correlated with destination depth for MM-3 ($r = 0.372$, $0.02 < p < 0.05$), and not correlated with destination depth for MM-1 ($r = 0.094$, $p > 0.2$). No statistically significant relationships were found between mean ascent rate and mean descent rate for any of the four whales (reported in Table 1). There was a significant difference between ascent rates (ANOVA, $p <$

Fig. 5. Percentages of time spent at depth from TDR data for MM-1 (*a*) and MM-2 (*b*) and adapted from Martin et al. (1994) (*c*). Only MM-1 and MM-2 provided sufficiently detailed data for making these comparisons. To facilitate comparison, data from this study were binned into the same depth bins as used in Martin et al. (1994).

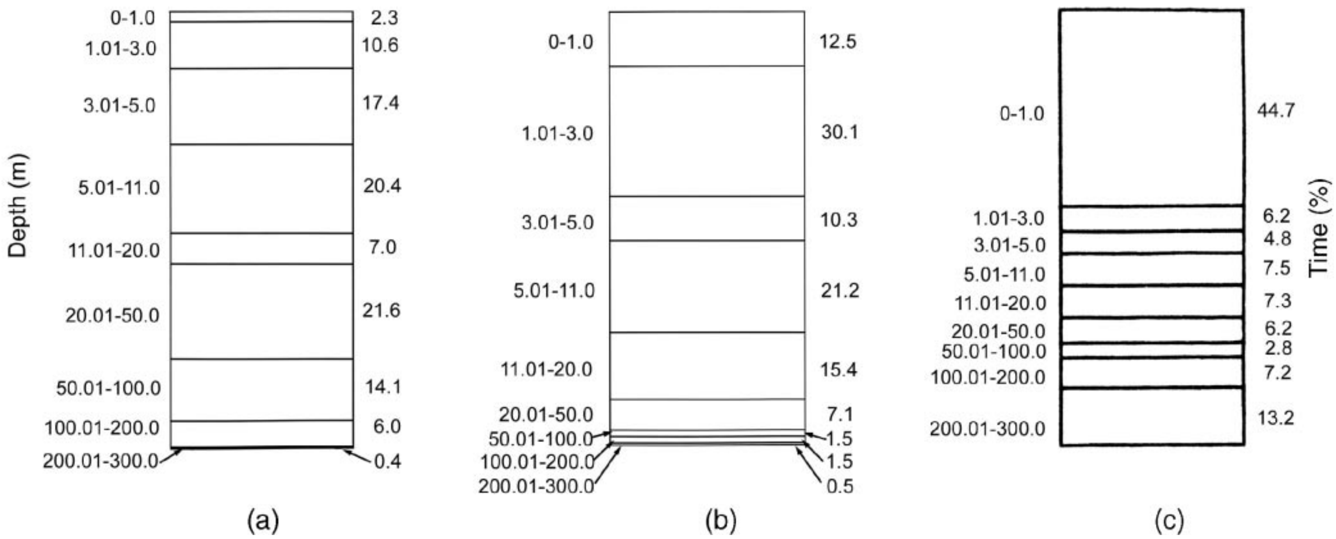


Table 2. Proportions of time spent at depth for two narwhals in Tremblay Sound, reported at a finer scale near the surface (1-m increments between 1 and 10 m).

Depth bin (m)	MM-1 (%)	MM-2 (%)
0–1.0	2.3	12.5
1.01–2.0	3.4	16.2
2.01–3.0	7.3	13.9
3.01–4.0	9.2	4.4
4.01–5.0	8.2	5.9
5.01–6.0	6.2	4.4
6.01–7.0	4.3	3.6
7.01–8.0	3.4	3.2
8.01–9.0	2.6	3.1
9.01–10.0	2.4	3.3
10.01–20.0	8.6	18.9
20.01–50.0	21.6	7.1
50.01–100.0	14.1	1.4
100.01–200.0	6.0	1.5
200.01–300.0	0.4	0.7

Note: These data are useful for determining correction factors for availability bias in aerial surveys, based on the proportion of time whales are at (or below) a specific depth.

0.001) and descent rates (ANOVA, $p < 0.001$) between individuals. A Tukey–Kramer post-hoc analysis revealed significant differences in both ascent and descent rates between MM-1 and the other three whales.

Proportion of time spent at different depths

Only the two tags from Tremblay Sound provided the resolution necessary for calculating the percentage of time spent within specific depth bins (Table 2). MM-1 and MM-2 spent approximately 49.3 and 70.5% of the time, respectively, within 10 m of the surface. It is clear that MM-1 spent more time at greater depths (between 20 and 100 m) than MM-2. Figures 5*a* and 5*b* (binned into intervals to match Martin et al. 1994) visually demonstrate that the whales were using the water column differently. MM-1 spent approximately one-fifth of the time in the 0–1 m depth category and approximately one-third of the time in the 1–3 m depth category that was spent by MM-2.

TDR and SLTDR comparison

Dive data from TDRs and SLTDRs deployed simultaneously were compared for three individuals (MM-1, MM-2, and MM-4) in this study. Because attachment times for the TDRs varied, only small amounts of data could be statistically compared. Although TDR attachment overlapped with thirteen 6-h periods for the three whales, we report only the results from full 6-h periods with complete TDR and SLTDR records, which were obtained as follows: one period for MM-1, one period for MM-2, and five periods for MM-4 (Table 3). Owing to the SLTDR set-up, for this comparison a dive was defined as >8 m for MM-1 and MM-4 and >12 m for MM-2.

Surface time was approximately 11% higher from the SLTDR than the TDR for MM-1, was 5% higher for MM-2, and varied for MM-4, the first two temporal periods being 2–3% higher for the SLTDR and the last three temporal periods approximately 1% lower (Table 3). Mean dive depth and mean dive duration from the SLTDR were lower (in all but one period) than the TDR data. When the five temporal periods were combined for MM-4 (the only individual on which the TDR remained for longer than a single 6-h period), there was no significant difference in mean depth and mean duration from the SLTDR and TDR data across periods ($p = 0.75$ for depth, $p = 0.44$ for duration).

Discussion

The recovery of the tags in Tremblay Sound was primarily due to the high cliffs in the area, which were used for long-range VHF signal detection. The recovery of the tags in Creswell Bay was primarily due to helicopter support, where VHF signal direction and strength could be located from an

Table 3. Comparison of dive statistics obtained for narwhals equipped with time–depth recorders (TDRs) and satellite-linked time–depth recorder (SLTDRs) simultaneously.

	MM-1 (*n* = 1)		MM-2 (*n* = 1)		MM-4 (*n* = 5)	
	TDR	SLTDR	TDR	SLTDR	TDR	SLTDR
Surfacing time (%)	36.6	47.9	55.2	60.8	68.2	71.7
					50.0	52.9
					47.9	47.1
					41.5	41.3
					47.2	46.3
Mean dive depth (m)	64.9	55.4	24.6	21.3	22.1	19.5
					38.8	35.6
					38.0	Incomplete
					40.7	40.8
					32.0	30.1
Mean dive duration (min)	5.9	4.6	2.7	1.6	2.8	2.1
					5.2	4.3
					4.4	3.7
					5.1	4.6
					4.1	3.4

Note: Dive summaries for individual periods are listed in separate columns; *n* is the number of complete 6-h periods when both tags were on the narwhal. For surfacing time, depth was set as <6 m for MM-1 and <7 m for MM-2 and MM-4. The depth to be considered a dive was >8 m for MM-1 and MM-4, and >12 m for MM-2.

altitude of approximately 2500 ft (1 ft = 0.3048 m). We observed no adverse reaction to the tagging procedure after release, such as prolonged periods at the surface that were not also observed hours into the tracking period or excessively slow movements in the water column. Dive depths and velocity were initially high once the whales were released; however, similar depths and speeds were observed hours into the data collection.

The whales instrumented with TDRs in both Tremblay Sound and Creswell Bay were physically restricted in diving beyond the maximum depths recorded here, owing to the relatively shallow habitat of their summering grounds. Studies have demonstrated that narwhals are capable of diving to depths >1500 m (Heide-Jørgensen et al. 2002). Most of these records come from the whales' wintering grounds in Baffin Bay and Davis Strait, where water depths reach >2500 m. The data presented in this study are probably representative of typical narwhal behaviour on their summering grounds, as other studies have reported similar dive statistics during the same season (Heide-Jørgensen and Dietz 1995; Heide-Jørgensen et al. 2001). It appears that narwhals use the deepest parts of the water column in both summering and wintering areas.

The two whales tagged in Tremblay Sound exhibited clear differences in diving behaviour that could not be attributed to sex or body size, as both whales were males in the same size class. In Tremblay Sound, MM-1 made longer, deeper dives and spent less time at the surface than MM-2 (Figs. 3*a*, 3*b*, and 5). The differences between the whales could be related to individual differences in foraging and diving capabilities or site-specific behaviour. Only MM-1 had a significant correlation between post-dive surfacing duration and dive depth, which has been interpreted as reaching an aerobic limit (Boyd 1997; Kooyman and Ponganis 1998). However, the correlation between post-dive surfacing duration and depth here may not indicate aerobic limitations, because much longer dives and deeper dive depths have been recorded for narwhals (Heide-Jørgensen and Dietz 1995; Heide-Jørgensen et al. 2002). There have been few studies on the aerobic limits of narwhals. Williams et al. (1987) calculated an aerobic dive limit (ADL) (the maximum dive duration that can be supported by aerobic metabolic processes) for a 1200-kg narwhal to be 14 min (at a swim speed of 1.5 m/s) or 21 min (at a swim speed of 1.0 m/s). Schreer and Kovacs (1997) also predicted a maximum dive depth (1000 m) and maximum dive duration (20 min) for narwhals on the basis of allometric equations related to body mass (estimated as 1600 kg). ADLs have also been examined for the beluga, *Delphinapterus leucas* (a close relative to the narwhal), and are similar. Schreer and Kovacs (1997) reported an ADL for a beluga of 25 min and Shaffer et al. (1997) reported a maximum dive duration for captive belugas of 13.3 min and an empirically determined ADL of 9–10 min.

MM-1 made two long dives that exceeded the duration threshold reported by both Williams et al. (1987) and Schreer and Kovacs (1997): one dive to a depth of 183 m dive that lasted over 26 min and another to a depth of 186 m that lasted slightly over 20 min. The durations for more than five dives made by this individual were longer than the maximum dive durations for narwhals reported by Silverman (1979) (14 min), Dueck (1989) (13 min), and Martin et al. (1994) (15.1 min). It is interesting to note that the dives which exceeded these reported thresholds were made in relatively shallow water and during the summer, a time when narwhals are not generally making their deepest, longest dives. Note, however, that the durations recorded for the other three whales in this study were shorter and more consistent with the reported literature.

The two narwhals tagged in Creswell Bay (MM-3 and MM-4) had similar diving behaviour. Both whales generally made short, shallow dives (<80 m), especially compared with the whales tagged in Tremblay Sound, which had dive depths and durations almost twice those in Creswell Bay. The depth in Creswell Bay is less than one-half the depth in Tremblay Sound, therefore these differences may be solely attributed to region. Sex-specific diving behaviour may be part of the explanation; however, inferences from this are confounded in this study because only one sex was captured at each site.

The positive correlation between depth and duration for all four whales is due to the longer travel time required to reach deeper depths. Dive rates for narwhals reported in Heide-Jørgensen and Dietz (1995) ranged from 7.9 dives/h (SD = 2.0 dives/h) to 11.2 dives/h (SD = 3.3 dives/h). Heide-Jørgensen et al. (2001) reported that dive rates ranged from 1 to 20 dives/h for narwhals, with a mean of 7.5 dives/h (SD = 3.4 dives/h). These rates are comparable to the rates reported here, ranging from 6.0 dives/h (SD = 2.2 dives/h) to 10.9 dives/h (SD = 1.2 dives/h).

Mean ascent and descent rates for all whales were not significantly different from one another (ANOVA, $p \geq 0.2$); however, significant differences were found between individuals, clearly influenced by MM-1. Distinct bursts of speed (an increase in ascent or descent rate) were not observed for any of the four whales. This suggests that whales were foraging in a fairly passive manner or not foraging at all. Behavioural and dietary studies indicate that narwhals feed little during the late summer (Finley and Gibb 1982), and it is presumed that whales feed more intensively as they move south to their wintering grounds. Therefore, the behaviour recorded here most likely does not include intense feeding bouts. Heide-Jørgensen and Dietz (1995) reported ascent and descent rates ranging from 0.6 to 2.1 m/s for narwhals equipped with SLTDRs, showing no clear trend in ascent and descent rates with increasing destination depth. It is possible that differences in ascent and descent rates in shallow water are less apparent than those recorded for whales diving in deeper water (e.g., Hooker and Baird 1999).

The consistency in dive profiles with little bottom time indicates that whales were not actively chasing prey under water. Statistical classifications of dive shapes and classifications have been published for several species (Schreer and Testa 1995; Lesage et al. 1999; Malcolm and Duffus 2000). We observed only a few dives where the direction and (or) shape changed in the water column. Most dives appeared to be V-shaped (Martin et al. 1994; Fig. 4) with minimal bottom time. It is possible that whales were merely travelling in and between bays and fjords in these regions, or if active foraging occurred, it was not when the whales were being monitored.

MM-1 and MM-2 spent 30.3 and 52.9% of their time at depths <5 m, respectively (Fig. 5). These data are fairly consistent with those from other studies. For example, Heide-Jørgensen and Dietz (1995) reported that 40% of the time spent by seven narwhals tagged in Melville Bay, west Greenland, was at depths <5 m (ranging from 35 to 64%). In addition, Heide-Jørgensen et al. (2001) reported the mean time spent at >5 m depth as 46.7% and mean time spent at >6 m as 64.0% for narwhals tagged in Tremblay Sound. Martin et al. (1994) reported the time spent at >5 m depth for one whale tagged in Tremblay Sound as 55.7%.

The proportion of time spent at water depths where narwhals can be visible during a standard aerial survey is of particular interest when estimating abundance. Generally, a correction factor is applied to aerial survey data to account for animals that are below the surface, or below depths where they could be counted from the air or seen in aerial photographs. Narwhals can be seen and positively identified from the air or in aerial photographs at depths of 2–5 m, and occasionally 7 m (Richard et al. 1994). Correction factors for availability bias to 5 m depth (calculated as 1/total time ≤ target depth) for MM-1 and MM-2 would be 3.3 and 1.9, respectively. For a maximum depth of 7 m, correction factors are 2.6 and 1.7, respectively. Martin et al. (1994) collected data on diving narwhals using a slightly different type of satellite-linked radio transmitter than those reported in Dietz and Heide-Jørgensen (1995) and Heide-Jørgensen and Dietz (1995) (which recorded data in a manner more similar to TDRs with a 40-s sampling frequency). Martin et al. (1994) calculated correction factors of between 1.8 (visibility to 5 m depth) and 1.7 (visibility to 7 m depth) for narwhals, based on his study. Another correction factor that has been calculated on the basis of time spent at depth during August and September is 2.5 for <5 m depth (Heide-Jørgensen and Dietz 1995). This is similar to our correction factors calculated for <5 m depth. Differences in correction-factor calculations can be attributed to the physical restrictions of the habitat (shallow vs. deep water) occupied by the whales when they were monitored. Note that MM-1 exhibited dive behaviour that was unlike that of MM-2, which resulted in a large range between the two estimates. Correction factors needed to account for biases in abundance estimates may vary depending on location and season. The depth at which a narwhal can be unambiguously detected is usually difficult to determine, as it depends on water turbidity, light conditions, glare, whale size, and whale behaviour.

Martin et al. (1994) also reported the proportion of time an adult narwhal spent at different depth bins in Tremblay Sound. Our data (Figs. 5*a*, 5*b*), when binned into the same categories, gave different results. These differences are not due to location or time of year because data were collected for both studies in Tremblay Sound in the month of August. However, it is possible that the difference can be attributed to sex-specific behaviour, since Martin et al. (1994) reported their data for a female whale. The tag used by Martin et al. (1994) sensed depth every 40 s and remained on the whale for 15.9 days. To account for differences in sampling rate (tags in this study sampled depth every 1 s), we resampled our data into 40-s increments and arrived at very similar proportions to the 1-s sampling rate.

Studies on pinnipeds comparing TDRs and SLTDRs generally report larger sample sizes (complete sampling periods with both instruments) because the instruments can be glued to the fur of the animal and retrieved easily. Our sample size used for the comparison here (seven full 6-h SLTDR periods) represents 42 h of suction-cup attachment on the whales, a relatively substantial sample size relative to other cetacean TDR studies (Hooker and Baird 1998; Baird et al. 2001). Recently, several studies have been published in which suction-cup-attached TDRs have been successfully deployed on and retrieved from cetaceans (Hanson and Baird 1998; Hooker and Baird 1999; Malcolm and Duffus 2000; Hooker and Baird 2001; Baird et al. 2001). In these studies, however, SLTDR data were not collected and compared on individuals simultaneously.

Our small sample size showed that the estimated proportion of time spent at the surface (between 0 m and a selected depth) is similar for both TDR and SLTDR data (Table 3).

These results are similar to that of Burns and Castellini (1998), who, despite a small sample size and a coarser sampling rate than that reported here, found that the two methods were generally comparable. Corroborating SLTDR surfacing data is very important for estimating cetacean abundance. Species-specific correction factors for cetaceans are generally obtained from SLTDR deployments or VHF surfacing signals. TDR data collected for cetaceans are particularly useful for developing correction factors because the high sampling rate (1 s) enables a detailed calculation of time spent at depth for each metre of the water column, whereas SLTDR data are measured every ≥10 s and summarized in crude categories. The high-resolution TDR data facilitate the use of a probability-estimation technique where availability at various depths can be quantified.

Both the mean dive depth and mean dive duration estimated from the TDRs were higher than (or in one case equal to) those estimated from the SLTDR for all complete sampling periods. There are two explanations for the lower means obtained from the SLTDR. The coarser sampling scheme of the SLTDR may underestimate depths and durations. In addition, the midpoint of a bin (a common technique for obtaining mean values from SLTDR data) most likely underestimates mean depths and durations. Overall, our findings suggest that dive data collected from the TDRs and SLTDRs are generally comparable. These findings come from a relatively small sample size, where TDR attachment time was shorter than that necessary for a robust analysis. Future work should target longer sampling periods for cetaceans so that results from these two types of tags can be compared.

The results of this study indicate that narwhals exhibit shallow diving behaviour on the summering grounds relative to their diving behaviour in winter in the deep waters of Baffin Bay. There appeared to be individual differences in dive parameters both within a region and between regions. There are many possible explanations for then differences, and clearly, more data are needed to resolve the disparity. TDR deployments have enabled the first detailed description of narwhal diving behaviour in two summering grounds in the Canadian High Arctic.

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