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Published in:
Marine Ecology - Progress Series

Link to article, DOI:
[10.3354/meps261269](https://doi.org/10.3354/meps261269)

Publication date:
2003

Document Version
Publisher's PDF, also known as Version of record

[Link back to DTU Orbit](#)

Citation (APA):
Laidre, K. L., Heide-Jørgensen, M. P., Dietz, R., Hobbs, R. C., & Jørgensen, O. A. (2003). Deep-diving by narwhals *Monodon monoceros*: differences in foraging behavior between wintering areas? *Marine Ecology - Progress Series*, 261, 269-281. DOI: 10.3354/meps261269

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Deep-diving by narwhals *Monodon monoceros*: differences in foraging behavior between wintering areas?

Kristin L. Laidre^{1,6,*}, Mads Peter Heide-Jørgensen^{2,4}, Rune Dietz³,
Roderick C. Hobbs⁴, Ole A. Jørgensen⁵

¹School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195, USA

²Greenland Institute of Natural Resources, Box 570, 3900 Nuuk, Greenland

³Department of Arctic Environment, National Environmental Research Institute, Frederiksborgvej 399, Boks 358, 4000 Roskilde, Denmark

⁴National Marine Mammal Laboratory, AFSC, 7600 Sand Point Way NE, Seattle, Washington 98115, USA

⁵Danish Institute for Fisheries Research, Charlottenlund Slot, 2920 Charlottenlund, Denmark

⁶Present address: National Marine Mammal Laboratory, AFSC, 7600 Sand Point Way NE, Seattle, Washington 98115 USA

ABSTRACT: Variation in resource selection among sub-populations may elucidate differences in fitness and life history strategies. Specifically for top marine predators, differences in movements and behavior may result from responses to variation in a patchy, dynamic environment. Satellite-linked time-depth recorders (SLTDRs) were used to examine differences in narwhal *Monodon monoceros* diving behavior and habitat selection among 3 sub-populations in Canada and West Greenland (n = 16 individuals). The number of dives to different depths and time allocation within the water column was investigated in 3 seasons, with a focus on 2 discrete wintering grounds in Baffin Bay. Diving parameters were calculated from binned dive data and analyzed using repeated-measures mixed models accounting for temporal autocorrelation and individual variability. The number of surface dives (0 to 50 m) and time at the surface declined between summer and winter. Clear differences were observed between 2 wintering grounds. Whales occupying one wintering ground spent most of their time diving to between 200 and 400 m (25 dives per day, SE 3), confirmed by both depth and temperature recording tags. In contrast, narwhals in a separate wintering ground spent less time at shallow depths and most of their time diving to at least 800 m (13 to 26 dives per day, SE 1 to 3). A model of occupancy time at depth showed that whales making multiple daily deep dives spent over 3 h at >800 m (SD 0.6) and traveled 13 min (SD 1) per round trip to reach this depth. Whales diving to between 200 and 400 m spent approximately 2.5 h (SD 0.4) at this depth, traveling 5 min per round trip. The observed differences in time allocation and dive behavior indicate local variation between the 2 wintering grounds in the Baffin Bay ecosystem.

KEY WORDS: Narwhal · Diving behavior · Migration · Arctic · Foraging · Baffin Bay

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INTRODUCTION

The narwhal *Monodon monoceros* is a year-round inhabitant of Arctic waters bordering the Atlantic Ocean. During July and August, narwhals are widely distributed in large expanses of open water fjord com-

plexes and bays in the eastern Canadian High Arctic and Northwest Greenland. Narwhals make annual long distance migrations between high Arctic summering grounds and wintering grounds farther south in deep, ice-covered waters in central Baffin and Davis Strait, which are occupied between November and

April (Dietz & Heide-Jørgensen 1995, Dietz et al. 2001, Heide-Jørgensen et al. 2002, 2003).

Multi-annual satellite tracking studies have demonstrated high site fidelity to migration routes and wintering grounds. Different sub-populations use specific migratory corridors and each year return to the same wintering ground (Dietz et al. 2001, Heide-Jørgensen et al. 2003). Thus far, 2 wintering grounds have been identified based on tagging operations conducted at 3 summering sites between 1993 and 2001. Narwhals tagged in Tremblay Sound, Canada (Eclipse Sound sub-population) and Melville Bay, West Greenland (Melville Bay sub-population) share a wintering ground in southern Baffin Bay - Northern Davis Strait, along the continental slope between 69° 30' N and 68° N at 58' W (Dietz et al. 2001, Heide-Jørgensen et al. 2002). Narwhals tagged in Creswell Bay, Canada (Somerset Island sub-population) winter in an area farther north in Baffin Bay, slightly west of the continental slope, between 69° 30' N and 70° 30' N at 63° W (Heide-Jørgensen et al. 2003). There does not appear to be any exchange of whales between wintering grounds (Dietz et al. 2001, Heide-Jørgensen et al. 2002, 2003).

Narwhal diving behavior has been examined using satellite-linked time-depth recorders (SLTDRs) (Heide-Jørgensen & Dietz 1995, Heide-Jørgensen et al. 2001) and time-depth recorders (TDRs) (Martin et al. 1994, Laidre et al. 2002). These instruments have been deployed during the limited open water season in August and September with varying attachment durations. Narwhals appear to make relatively short, shallow dives in summer (depths are limited by their surrounding habitat) (Heide-Jørgensen et al. 2002, Laidre et al. 2002) and increase dive depth and duration in the fall (Heide-Jørgensen et al. 2001). Whales move quickly to their wintering grounds during a 2 mo migration period. On the wintering grounds, narwhals are relatively stationary for 6 mo, moving around locally with the shifting leads and cracks in the pack ice. It is in this habitat that they have been noted to make the deepest dives (Heide-Jørgensen & Dietz 1995, Heide-Jørgensen et al. 2002).

Seasonal differences in dive behavior between sub-populations of narwhals have not been quantified, and it is not clear how behavior may be influenced by summering ground origin or wintering ground location. Information on habitat use during the winter period and divergent behavioral characteristics between sub-populations is critical both due to the potential development of an offshore, deep-water fishery for Greenland halibut *Reinhardtius hippoglossoides* on the wintering grounds, and also in the context of increasing sea ice on the wintering grounds due to climate change (Parkinson et al. 1999, Deser et al. 2000, Stern

& Heide-Jørgensen 2003). Sub-population discreteness, together with high site fidelity to wintering grounds, provides the opportunity to examine and contrast the ecology of narwhal foraging in different areas.

Boyd (1997) describes a dive in the context of a single unit of animal behavior: an individual makes an excursion from the surface to capture food in a specific period of time before returning to the surface to breathe. Consequently, foraging time in the water column is the time remaining between the start of the dive, the transit time down to the destination depth(s) and transit time back to the surface. Transit time is correlated with destination depth and air-breathing mammals that choose to transit to deep depths consequently limit their foraging time underwater due to physiological constraints. If an animal chooses to make frequent deep dives over a long period of time, it may be indicative that the potential benefit from diving to those depths is greater than the trade-offs. This idea provides a framework for testing how behavioral changes compare to relative trade-offs of diving to different depths.

This study utilized dive records collected from satellite tags deployed on narwhals in 3 localities to contrast differences in seasonal trends in dive behavior between sub-populations, with a focus on the winter period. Data from multiple individuals tagged at different sites were compiled to quantify the frequency of dives to various depths and the prevalence of deep diving in the daily time budget. A time allocation model partitioned time in depth categories into surface time, transit time and occupancy time, and was used to examine the trade-offs of utilizing different depths.

MATERIALS AND METHODS

Field operations. Narwhals were caught using nets set perpendicular to the shoreline (details described in Dietz et al. 2001). Three types of tags were used: Telonics (Mesa, AZ) and Seimac (Canada) SLTDRs with approximately 0.5 W power output; programmed and cast in epoxy by Wildlife Computers (Redmond, WA), and Wildlife Computers SPOT2 satellite position only tags, recording geographic position together with proportion of time spent in temperature categories. Transmitters were attached to female whales on the dorsal ridge with two or three 5 to 8 mm polyethylene or titanium pins. Transmitters were attached to the tusk of males using 2 stainless steel bands (Seimac SSC3 or the Telonics ST-6 transmitter unit programmed and cast by Wildlife Computers). Transmitter longevity, influenced by a number of factors, varies with individual, and consequently individuals were not tracked for the same duration of time.

Location data. A single daily Argos position (location quality 1 to 3) was selected for each whale during the peak satellite passage (15:00 h local time). The temporal period between daily positions for individuals was approximately 24 h (SD 2 h) and positions were selected with priority given to equal temporal spacing to avoid spatial autocorrelation. Location data were imported into ESRI ArcINFO 8 and linked with a depth value obtained from a 2.5 km grid (International Bathymetric Chart of the Arctic Ocean). Depth values at the whale locations on the wintering grounds were summarized and compared using student *t*-tests.

Dive data. Data were collected from narwhals around Baffin Island and Somerset Island, Canada between 1997 and 2001, and were combined with rel-

evant records from previous published studies conducted in West Greenland in 1993 and 1994 (Dietz & Heide-Jørgensen 1995, Heide-Jørgensen & Dietz 1995). Sixteen narwhals were used in the analysis (6 M and 10 F) where tag attachment lasted well into the late migration or winter period (defined here as beyond Nov 1, based on Heide-Jørgensen et al. 2002). Thirteen whales were equipped with tags with pressure sensors and 3 whales were equipped with tags with temperature sensors. Data for each whale were divided into 3 seasons: summer (tagging date to 15 Sep), autumn migration (16 Sep to 31 Oct) and winter (1 Nov until end of tag transmissions) and whales were assigned to 1 of the 2 wintering grounds based on their destination (Fig. 1). All tags were deployed between 16 August and 2 September. Pres-

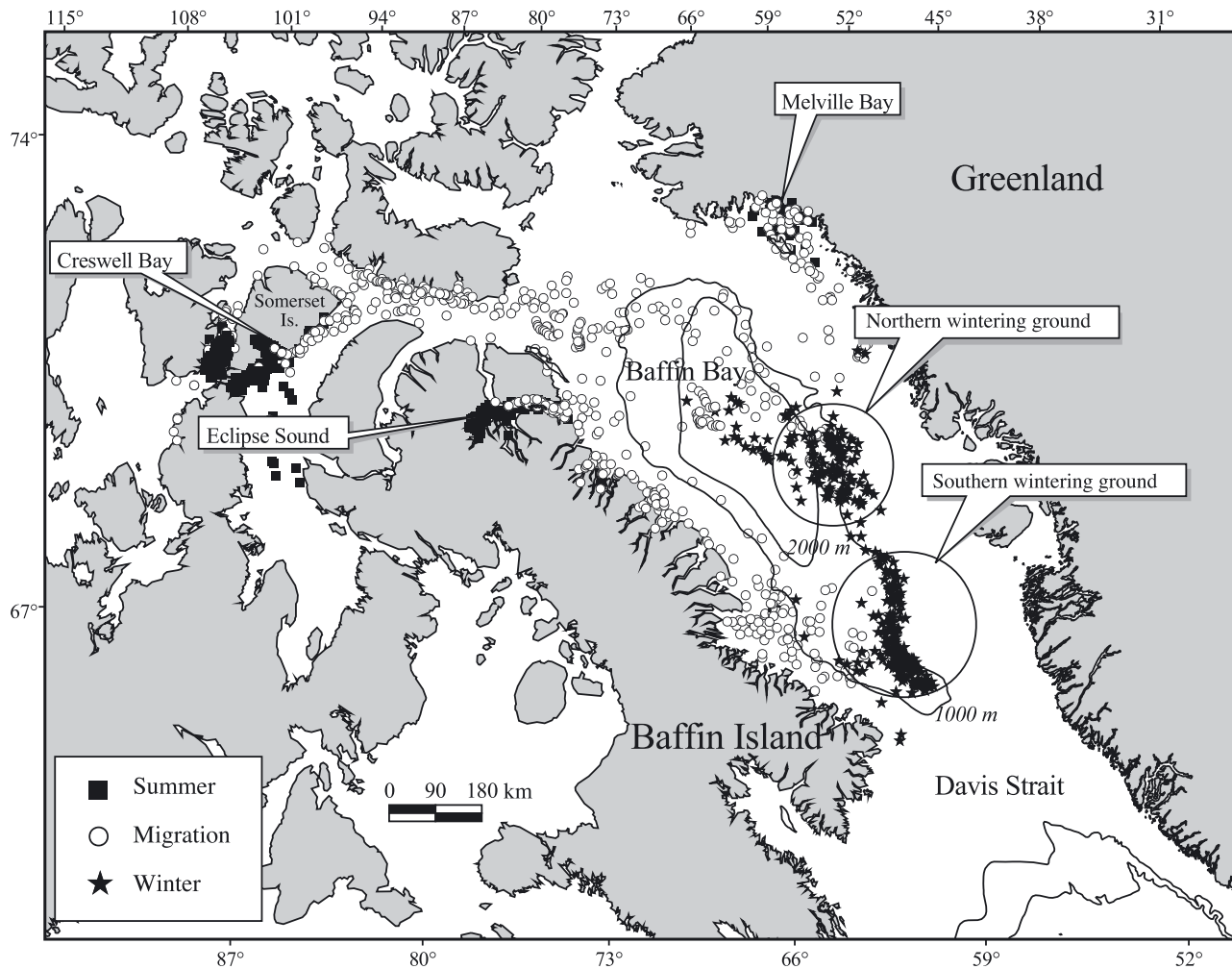


Fig. 1. Locality names, wintering grounds and location data collected from 16 satellite tags from each of 3 summering grounds (Creswell Bay, Tremblay Sound and Melville Bay). Positions are classified according to the 3 seasons in this analysis: summer (tagging to 15 Sep), migration (16 Sep to 31 Oct), and winter (1 Nov until end of tag transmissions). Narwhals tagged in Tremblay Sound are from the Eclipse Sound sub-population, narwhals tagged in Creswell Bay are from the Somerset Island sub-population and narwhals tagged in Melville Bay are from the Melville Bay sub-population. The 1000 and 2000 m contours are shown for reference

sure transducers sampled the depth of the whale at 4 m (0 to 1000 m range) or 6 m (0 to 1500 m range) resolution depending on the tag model and year of deployment. SPOT2 tags collected binned 'time at temperature' histograms by sampling temperature every 10 s and accumulating proportion of time a whale spent within several water temperature categories (or 'bins') between -2 and $+3^{\circ}\text{C}$. Data on the number of dives in different maximum depth categories and the proportion of time spent in the depth categories were collected in four 6 h periods across each day and summarized into histograms with up to 14 depth categories. Only 6 h periods with available information on the number of dives and the time at depth were used in the analysis. Intervals between surfacings were not considered dives unless a depth of >8 m was recorded (with the exception of 2 individuals where dives started as 12 m) (Table 1). Time spent within a depth category with a duration of <10 s may have been missed because depth data were sampled at that temporal resolution. Dive data were transmitted in segments when the whale surfaced, and were re-assembled using Wildlife Computers software packages (SATPAK). Time spent in different temperature categories by 3 whales during

winter 2001 was related to water depth using CTD casts taken in October 2001 on the northern wintering ground (Jørgensen 2002).

Absolute or total time in each time at depth category was partitioned into transit and occupancy time by calculating the time spent in each destination depth category (occupancy time) once the time spent on the vertical transit through the depth category to other depths was removed (transit time). Dives to deeper depths were assumed to be composed of either time spent transiting to and from that depth or time spent foraging, similar to the 'U-shaped or square' dive model (Martin et al. 1998, Lesage et al. 1999, Schreer et al. 2001). The time budget model assumed that each dive incremented in the histogram counter originated from the surface and was directed towards a specific depth category, and that the individual remained between the upper and lower limits of that depth category when not transiting.

Data from 12 male and female narwhals tagged in Eclipse Sound, Canada between 1997 and 1999 were analyzed to identify potential sex-based biases in dive behavior, particularly deep diving ability. Because the tags with longer duration were not equally distributed across the 2 sexes, a larger sample size (including tags

Table 1. *Monodon monoceros*. Statistics on satellite tagging results for individuals in this study. Narwhals in 2001 were equipped with satellite position-only tags recording 'time at temperature' data and only the winter period was investigated. All other tags recorded dive depth and time at depth data using pressure transducers. Resolution of all tags was 4 m with the exception of 3961-98 and 3964-99 (6 m). The number of complete 6 h periods collected during each season is shown. 'Summer' represents tagging to 15 September, 'migration' is 16 September to 31 October, and 'winter' is 1 November until end of tag transmissions. Locations were received for some days where complete 6 h periods were not received; therefore, the number of days reported here does not represent tag longevity

Locality	ID-Year	Longevity (Day of Year)	Sex/size (cm)	Summer (6 h periods)	Migration (6 h periods)	Winter (6 h periods)	Total (6 h periods)
Melville Bay	3960-93	245–332	M >400	55	184	–	239
Melville Bay	20167-94	239–343	M 405	27	96	103	226
Eclipse Sound	6335-97	236–312	M 440	64	124	15	203
Eclipse Sound	20162-98	234–396	M 475	83	141	177	401
Eclipse Sound	3961-98	238–308	M 500	77	129	–	206
Eclipse Sound	3964-99	233–450	M 410	99	182	397	678
Eclipse Sound	29689-99	227–355	F 405	126	179	–	308
Somerset Island	7927-00	227–324	F 390	120	184	78	382
Somerset Island	7928-00	227–296	F 370	128	126	–	254
Somerset Island	20683-00	230–300	F 390	79	114	–	193
Somerset Island	20688-00	230–348	F 402	94	133	87	314
Somerset Island	20689-00	230–333	F 397	104	157	97	358
Somerset Island	20690-00	232–317	F 398	59	61	–	120
Somerset Island	7927-01	227–359	F 420	–	–	85	85
Somerset Island	20167-01	227–359	F 390	–	–	85	85
Somerset Island	20690-01	227–319	F 410	–	–	15	15
Total				1115	1810	1139	4067
Mean (SD)				86 (30)	139 (36)	114 (109)	254 (159)
Minimum				27	61	15	15
Maximum				128	184	397	678
n				13	13	10	16

with shorter duration) was used to examine the number of dives to different depths and time spent at different depths for males and females (ANCOVAs with date as a covariate).

Vertical speeds. Vertical speeds were inferred from the simultaneously recorded time at depth data and the number of dives to different destination depth categories. Vertical speeds could be estimated when a destination depth category (i.e. a depth category with the deepest dive) was isolated from previous depth categories by at least 1 transit depth category (i.e. the category the whale passed through to reach the destination category). The isolated transit categories facilitated both the count of the number of dives that went through the transit depths and the incremented amount of time spent passing through the transit categories. Vertical speeds to destination depths (\bar{S}_j where j = depth category) were calculated based on the model developed in Heide-Jørgensen et al. (1998):

$$S_j = \frac{N \times D \times 2}{\text{TAD}} \quad (1)$$

where N is the number of dives to an isolated dive destination category, D is the vertical distance (in m) across the transit depth categories to the isolated destination depth, and TAD is the sum of time-at-depth measurements (in s) through the transit depth categories. Average vertical speeds (\bar{S}_j) were calculated for all dives to each isolated depth category from narwhals tagged between 1993 and 2000, and were compared to speeds obtained from TDRs (Laidre et al. 2002). The vertical speeds were used to calculate the total time required to reach target depths and return to the surface, as well as total time spent transiting through different depth categories to reach a destination depth. Vertical transit speeds (m s^{-1}) were assumed to be constant from the surface to the destination depth. Average speeds for dives to depths <50 and >800 m were used in the model with all other depths assigned a specific vertical speed.

Transit time. Two aspects of transit time were estimated for each individual whale: the average time per day spent transiting through each depth category (j) (TransitTime $_j$) and the average round-trip transit time per dive to depth (j) (RTTime $_{\text{dive}_j}$). TransitTime $_j$ was defined as the sum of the overall time spent in each depth category that could be accounted for by the whale transiting through the water column to reach each of the deeper depth categories, or:

$$\text{TransitTime}_j = 2 \times \sum_{i=j+1}^k \bar{D}_i \times \frac{\text{DepthCatDist}_j}{\bar{S}_i} \quad (2)$$

where \bar{D}_i is the average number of dives per day to the i th depth category, k is the index of the deepest depth

category, DepthCatDist $_j$ is the vertical length (in m) between the upper and lower limits of the j th depth category, and \bar{S}_i is the average vertical speed from the surface (in m s^{-1}) to the i th depth category.

RTTime $_{\text{dive}_j}$ was defined as the time (min) between departure from the surface (where a dive was defined by the tag set-up) to the target depth and back to the surface, or:

$$\text{RTTime}_{\text{dive}_j} = [(\text{DiveDist}_j / \bar{S}_j) / 60] \times 2 \quad (3)$$

where DiveDist $_j$ is the distance from the surface to the upper bound of the depth category.

Occupancy time and total time. Occupancy time (OT $_j$), the average number of minutes spent in each category per day excluding time spent transiting through the category, was estimated for each individual, or:

$$\text{OT}_j = \frac{\text{TotalTime}_j - \text{TransitTime}_j}{60} \quad (4)$$

where TotalTime $_j$ was the total number of minutes spent in each category per day. The average number of minutes spent in the depth bin on each dive (OT $_{\text{dive}_j}$) was simply occupancy time divided by the mean number of dives per day to that depth bin, or:

$$\text{OT}_{\text{dive}_j} = \frac{\text{OT}_j}{\bar{D}_j} \quad (5)$$

The total time (min) for a dive to category $_j$ (TotalTime $_{\text{dive}_j}$), including transit time up and down from the surface and time spent in category $_j$, was then:

$$\text{TotalTime}_{\text{dive}_j} = \text{OT}_{\text{dive}_j} + \text{RTTime}_{\text{dive}_j} \quad (6)$$

Repeated-measures mixed models for number of dives and proportion of time at depth (converted to absolute time at depth in hours) were created using the LME procedure in S-PLUS Version 6.0. The repeated measure analysis accounted for temporal autocorrelation in the data and a random effect of individual variability in diving behavior between whales. Different spatial autocorrelation structures were explored (with and without a nugget), and temporal autocorrelation between days was ultimately modeled using a linear spatial autocorrelation structure with no nugget, which provided the best fit to the data. Individual whales were subjects in the autocorrelation model and a single model was fit for all whales for each depth category. The best model was determined using a forward stepwise procedure, with fixed effects (season, and summering locality or wintering ground) and the best model was chosen using Akaike's Information Criteria (AIC). Depth categories with prominent differences in number of dives and time at depth were identified for each season and further investigated.

Table 2. *Monodon monoceros*. Bottom depth (m) recorded at daily good quality ARGOS locations for individuals (ID-Year). Data are reported as mean (SD) and range. Empty values indicate no locations were obtained for those whales during that specific time period

Narwhal ID	Summer			Migration			Winter		
	Eclipse	Melville	Somerset	Eclipse	Melville	Somerset	Eclipse	Melville	Somerset
3960-93	91 (92)	10–232	368 (390)	3–1673	784 (251)	303–1277			
20167-94	360 (321)	7–970	664 (295)	37–1000	986 (181)	592–1350			
6335-97	644 (136)	302–814	762 (617)	34–1916	1485 (203)	1194–1643			
20162-98	319 (233)	9–669	748 (382)	14–1989	1321 (199)	628–1726			
3961-98	419 (244)	9–711	573 (457)	37–1698	517 (77)	453–603			
3964-99	422 (165)	98–668	450 (358)	33–1705	1403 (142)	995–1769			
29689-99	209 (200)	6–583	513 (240)	43–1083	–	–			
7927-00	323 (146)	38–467	435 (358)	24–2035	2297 (57)	2143–2355			
7928-00	97 (66)	18–284	436 (373)	49–2003	–	–			
20683-00	160 (80)	13–333	935 (623)	220–2198	–	–			
20688-00	81 (90)	4–367	877 (757)	41–2364	940 (483)	380–1949			
20689-00	42 (31)	2–91	850 (700)	22–2370	1580 (436)	23–664			
20690-00	209 (185)	5–458	953 (728)	123–2242	1344 (554)	559–2154			
7927-01	317 (161)	8–452	785 (749)	11–2291	1238 (517)	591–2348			
20167-01	265 (173)	5–441	805 (776)	48–2353	2014 (341)	575–2285			
20690-01	268 (163)	2–435	1033 (810)	146–2348	–	–			
Grand mean	265 (209)	2–970	699 (601)	3–2370	1362 (476)	303–2355			

RESULTS

The 13 dive data tags had a mean attachment time of 106 d (SD 43). The 3 SPOT2 tags had a mean attachment of 124 d (SD 27). The mean number of complete 6 h periods obtained from the whales during summer, migration and winter was 86 (SD 30, range 27 to 128), 139 (SD 36, range 61 to 184) and

114 (SD 109, range 15 to 397), respectively (Table 1). The selection of a single threshold date to identify the end of the summer period (Sep 15) was based on the later departure of whales from the summering ground in Melville Bay, and encompassed the typical summer behavior of whales for all 3 sites.

Locations relative to bottom depth

Daily good-quality ARGOS locations for the 16 whales (n = 1498 positions) were used to examine differences in depth selection between individuals by sex and season (Table 2). A grand mean of maximum bottom depth including all positions across all seasons was 731 m (SD 629, range 2 to 2370 m), and means for each season were 265 m (SD 209) for summer,

699 m (SD 601) for migration and 1362 m (SD 476) for winter. There was a significant difference between depths used by whales in the northern and southern wintering grounds (p < 0.001). Whales in the northern wintering ground were located in deeper water (1538 m, SD 637, range 380 to 2355 m) than those in the southern wintering ground (1252 m, SD 291, range 303 to 1769 m).

Table 3. *Monodon monoceros*. Repeated-measures mixed model parameter estimates (with SE) based on an interaction model between season and locality for each of 7 depth categories. A random effect of individual behavior and an effect of linear temporal autocorrelation between days (without a nugget) were included in the models. Average number of dives per day and absolute time at depth (h) in 3 seasons for each of 3 narwhal sub-populations are reported

Depth bin (m)	Summer			Migration			Winter		
	Eclipse	Melville	Somerset	Eclipse	Melville	Somerset	Eclipse	Melville	Somerset
Average number of dives per day									
0–50	159 (28)	167 (63)	149 (25)	147 (27)	165 (61)	101 (25)	116 (28)	151 (61)	59 (26)
50–100	8 (3)	11 (8)	15 (3)	7 (3)	6 (7)	10 (3)	10 (3)	13 (7)	11 (3)
100–200	4 (4)	7 (8)	8 (3)	5 (4)	4 (8)	14 (3)	10 (4)	5 (8)	19 (4)
200–400	11 (3)	14 (6)	9 (2)	7 (3)	12 (6)	20 (2)	5 (3)	3 (6)	25 (3)
400–600	11 (3)	5 (6)	6 (3)	12 (3)	6 (6)	10 (2)	3 (3)	2 (6)	12 (3)
600–800	4 (1)	10 (2)	0 (1)	7 (1)	10 (2)	2 (1)	2 (1)	4 (2)	2 (1)
>800	1 (1)	1 (2)	0 (1)	3 (1)	13 (2)	1 (1)	13 (1)	26 (3)	5 (1)
Average absolute time at depth per day (h)									
0–50	16.8 (0.8)	15.6 (1.9)	19.3 (0.7)	15.8 (0.8)	13.7 (1.8)	15.6 (0.7)	13.9 (0.8)	11.8 (1.8)	12.7 (0.8)
50–100	1.1 (0.2)	1.3 (0.4)	1.4 (0.1)	1.0 (0.2)	0.9 (0.4)	1.5 (0.1)	1.3 (0.2)	1.6 (0.4)	1.9 (0.2)
100–200	1.4 (0.2)	1.8 (0.6)	1.1 (0.2)	1.4 (0.2)	1.5 (0.5)	2.2 (0.2)	1.6 (0.2)	1.4 (0.5)	3.4 (0.2)
200–400	2.6 (0.5)	3.2 (1.3)	1.8 (0.5)	2.5 (0.5)	3.2 (1.2)	3.3 (0.5)	1.7 (0.5)	2.6 (1.2)	3.6 (0.5)
400–600	1.5 (0.2)	1.0 (0.6)	0.3 (0.2)	2.0 (0.2)	1.4 (0.6)	1.0 (0.2)	1.5 (0.3)	1.4 (0.6)	1.3 (0.3)
600–800	0.4 (0.1)	0.9 (0.3)	0 (0.1)	0.9 (0.1)	1.7 (0.2)	0.2 (0.1)	1.0 (0.1)	1.8 (0.2)	0.4 (0.1)
>800	0.1 (0.1)	0.1 (0.3)	0 (0.1)	0.4 (0.1)	1.5 (0.3)	0.1 (0.1)	3.0 (0.1)	3.3 (0.3)	0.7 (0.1)

Number of dives to depth

The stepwise approach resulted in the most parsimonious model with individual whales as random effects and an interaction between season and locality (either summering sub-population or wintering ground). Temporal autocorrelation in dive behavior between days was weak. The range of the correlation model (point on x-axis corresponding to y -value model asymptote) was between 1.3 and 1.5 d based on summering or wintering locality. Introduction of a nugget did not affect the range of correlation, but slightly increased the AIC values. The estimate of the total error variance in each model could be broken into 50% of the variance due to random behavior by individual whales and 50% from the residual. The interaction with season and summering sub-population produced better fits (lower AIC values) than the interaction with season and wintering ground for all depth categories.

Parameter estimates of the average number of dives per day to different depth categories displayed clear seasonal patterns, which in some seasons appeared to be divergent for sub-populations (Table 3). Near surface dives between 0 and 50 m made up the largest proportion of dives and these excursions are assumed to represent a variety of typical cetacean behaviors such as travel, resting, or milling besides near-surface foraging. The average number of these dives declined between summer and winter for the 3 sub-populations (reduced by approximately 50%) (Table 3). These near-surface dives were excluded from analyses when examining dives to deeper depths. Although the number of dives to different depths varied in summer and during migration for the 3 sub-populations, the overall patterns were similar with the most pronounced seasonal differences detected during the winter period. Narwhals from Somerset Island (390 to 402 cm length) made many more dives to mid-water depths than narwhals from both Eclipse Sound (410 to 475 cm) and Melville Bay (>400 cm), yet deeper dives were the apparent preference for the sub-populations from Melville Bay and Eclipse Sound (Fig. 2). A selection of mid-water depths farther north was clearly in contrast to selection of deep depths farther south.

In winter, 3 male narwhals from Eclipse Sound dove approximately 13 times per day to depths >800 m (SE 1), yet made only 5 dives (SE 3) to the mid-water depth category of 200 to 400 m (Fig. 2a). Narwhals from Melville Bay made 26 dives per day to >800 m (SE 3), yet this sub-population only made 3 dives per day (SE 6) to between 200 and 400 m (Fig. 2b). In contrast, Somerset Island narwhals made 25 dives per day (SE 3) to the 200 to 400 m depth category. The number of dives per day to deeper depths (>800 m) for this sub-population was 5 dives per day (SE 1) (Fig. 2c). The

95% confidence interval (CI) encompassing the parameter estimates for deep dives for both Eclipse Sound and Melville Bay did not overlap with the 95% CI for Somerset Island for this depth category. One of the whales from Eclipse Sound was equipped with a tag capable of recording very deep dives (>1400 m). When

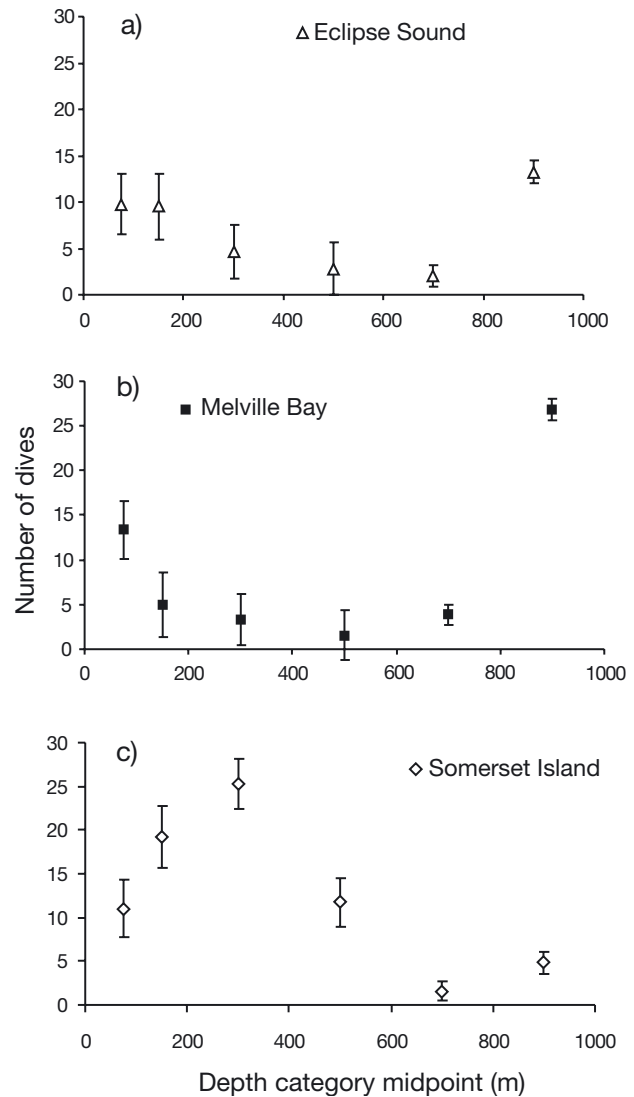


Fig. 2. *Monodon monoceros*. Parameter estimates (\pm SE) of the average number of dives per day to different depth categories for narwhals tagged at 3 different summering grounds excluding surface dives (<50 m). (a) Eclipse Sound, (b) Melville Bay, (c) Somerset Island. Estimates were derived from a repeated-measures model on each depth bin. Narwhals from the Melville Bay and Eclipse Sound winter in the southern wintering ground, whereas narwhals from the Somerset Island winter in the northern wintering ground. Note the large proportion of dives between 200 and 400 m for narwhals from Somerset Island in winter, and the large proportion of dives >800 m for narwhals from Melville Bay and Eclipse Sound in the same season. In both wintering areas, water depth ranges from 400 to over 1750 m

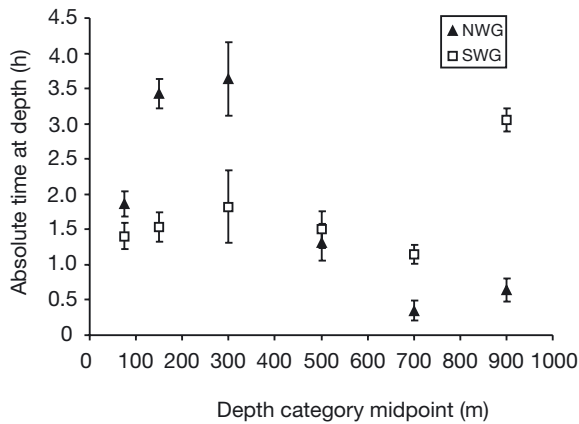


Fig. 3. *Monodon monoceros*. Model estimates of the absolute time at depth (\pm SE) during the winter period for narwhals occupying the northern and southern wintering ground, excluding time spent above 50 m. Estimates were derived from a repeated-measures model on each depth bin. 'NWG' stands for northern wintering ground and 'SWG' stands for southern wintering ground

the 13 dives per day >800 m for this whale were examined at this resolution, almost 50% of the dives exceeded 1400 m (6 dives, SD 0.5). Furthermore, 5 dives per day reached 1200 to 1400 m (SD 0.4), 1 dive per day between 1000 and 1200, and 1 dive per day between 800 and 1000 m. Upon examination of models for pooled whales on the 2 wintering grounds, a clear focus on dives to >800 m was found on the southern wintering ground (16 dives d^{-1} , SE 1.5), whereas fewer deep dives (5 dives d^{-1} , SE 1.6) and 5 times as many mid-water dives (25 dives d^{-1} , SE 3) were estimated to occur on the northern wintering ground.

The sex-specific dive behavior comparison including tags with shorter longevity during the summer and autumn migration period (13 Aug to 1 Nov) was based on 2106 periods of 6 h, examined for differences in the number of dives to different depth categories for males ($n = 4$) and females ($n = 8$). When dives to depths of 400 m and greater were examined at 100 m increments, significant differences between sexes were found in the 500–600 m depth category ($p = 0.01$), 700–800 m depth category ($p = 0.004$) and >900 m ($p < 0.001$) depth category (ANCOVA). In all cases, females performed significantly more dives per day to these depths than males. When the number of dives to deeper depth bins were pooled and males and females compared, both for dives >600 and >700 m, females made more deep dives per day than males (ANCOVA, $p < 0.001$ for >600 m, $p < 0.001$ for >700 m). In general, these results suggest no differences in diving performance between males and females, except that females make more dives to deeper depths than their male counterparts.

Absolute proportion of time at depth

Model estimates of the absolute proportion of time spent in each depth category (in hours) by season followed similar patterns as those observed with number of dives (Table 3), where time spent between 0 and 50 m declined from summer to winter. The parameter estimates of absolute time at depth per day by wintering ground (Fig. 3) demonstrated striking differences between the allocations of time in the water column. In the northern wintering ground, the largest proportion of time was spent between 200 and 400 m (over 3.6 h, SE 0.5), with a steep decline towards deeper depths, where on average, whales spent slightly over 0.7 h (SE 0.1) >800 m. In contrast, on the southern wintering ground, whales spent over 3 h d^{-1} (SD 0.1) at depths >800 m (6 times more than the northern wintering ground), and between 1.4 (SE 0.6) and 2.6 h (SE 1.2) d^{-1} at depths between 100 and 400 m, which include the time spent traveling through these depths to reach the >800 m destination depths (Fig. 3). Data collected from the high-resolution tag from Eclipse Sound indicated that of the daily average of 3 h >800 m in the winter, 30 min were spent at depths >1400 m, 45 min spent between 1200 and 1400 m, 48 min between 1000 and 1200, and 52 min between 800 and 1000 m.

Sex-specific differences in the proportion of time spent at different depths were examined for Eclipse Sound during the same period. The proportion of time spent at depths >400 m was examined incrementally by 100 m (ANCOVA). In most cases, there were no significant differences between the time spent for males and females. The one exception was the depth category of 500 to 600 m, where significant differences were found ($p < 0.001$) with males spending more time at this depth. In general, there was little difference between the time spent at different depths for males and females.

Proportion of time in temperature ranges

Three female narwhals collected time at temperature data on the northern wintering ground in 2001. After November 1, the proportion of time spent in specific temperature categories was concentrated in 2 ranges: 34% of the time was spent between -1.2 and -1.6°C (SD 15) and 25% of the time was spent between 0.3 to 1.7°C (SD 11) (Fig. 4). The lowest proportion of time (2%) was in the warmest temperature category, between 2.3 and 2.8°C . Two CTD casts, taken on the northern wintering ground in 2001 (Fig. 5), showed that the warm temperature category (2.3 to 2.8°C) occurred in 2 depth ranges: 0 to 20 m (Fig. 5 inset) and 300 to 600 m. In November and December 2000, whales in the

northern wintering ground spent on average 34 % (SD 8) of their time at depths <8 m (based on 165 periods of 6 h of surfacing data after November 1). Given this surfacing time estimate, even if the surface water cooled between the CTD measurements in the month of October and the whales' arrival in the month of November, the proportion of time spent in the 3 warmest depth categories (31%) does not allow for much diving behavior below 350 m, as whales must pass through this warm water thermocline layer to reach depths greater than 600 m, corroborating dive behavior recorded in 2002 using direct depth measurements.

Dive profiles and occupancy time

Vertical speeds were calculated from 1587 dives with a terminal destination depth from narwhals tagged between 1993 and 2000. The magnitude of the speed was significantly related to the destination depth and the vertical distance of the interval over which the speed was calculated (Fig. 6). Note, there were no female narwhals with 1500 m resolution tags; therefore, no estimates of speeds beyond 850 m are available for this sex. An average vertical speed was used in the time budget model between 0 and 50 m (0.41 to 0.45 m s⁻¹) and to depths of 800 m and greater (1.86 m s⁻¹) (Fig. 6).

Average daily occupancy time in each depth category (AOT_j) varied significantly between wintering

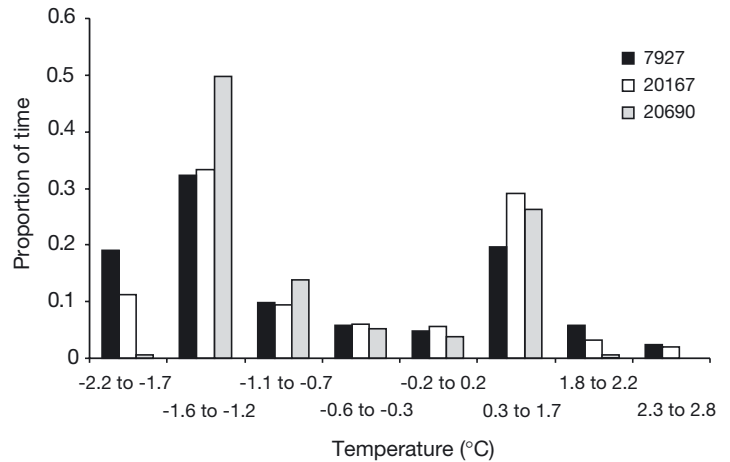


Fig. 4. *Monodon monoceros*. Histogram of the distribution of time-at-temperature during the winter for 3 narwhals tagged in Creswell Bay in 2001. Satellite-linked 'time at temperature' recorders increment temperature into categories every 10 s. Results were taken from 185 6-h periods collected after 1 November. Note that only 2% of the time was spent at temperatures >2.3°C, and when average surface time (proportion of time spent at depths <8 m) was accounted for, travel through this category on deep dives was seldom possible

grounds (Table 4). Whales in the northern wintering ground spent, on average, over 2.6 h d⁻¹ (SD 0.4) occupying the 200 to 400 m depth category, while whales on the southern wintering ground spent, on average, only 0.6 h d⁻¹ at this depth (SD 0.4). In contrast, whales in the

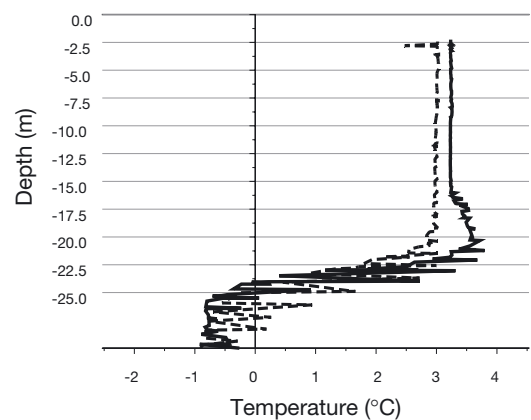
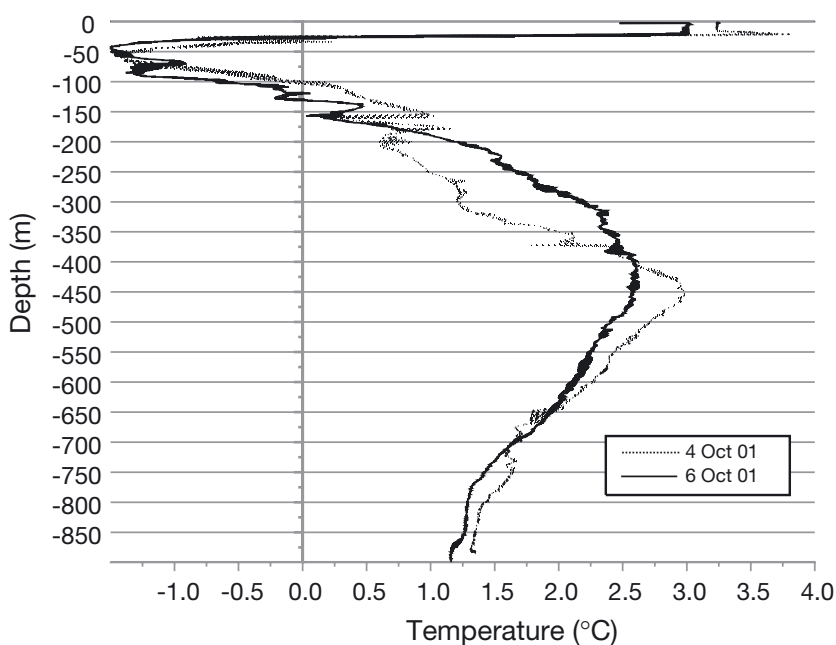


Fig. 5. CTD cast profiles taken on the northern wintering ground in October 2001. Casts were taken at 72° 3.5' N, 60° 17.3' W and 71° 19.3' N, 60° 21.9' W. Right profile shows detailed temperature gradient at near surface depths (<20 m). Note the thermocline (temperatures >2.3°C) between 300 and 600 m, which narwhals must pass through to make dives deeper than 600 m

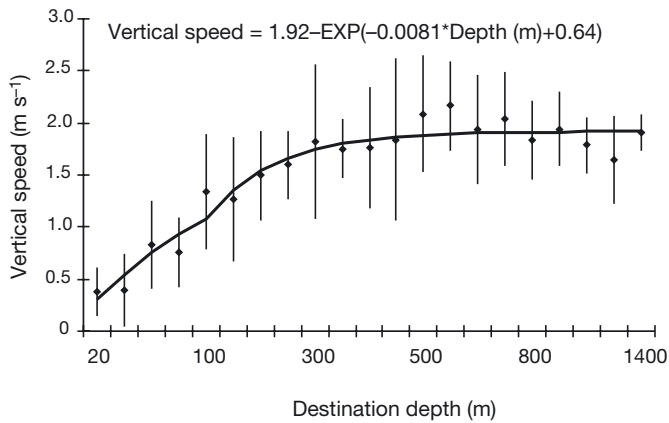


Fig. 6. *Monodon monoceros*. Estimates of mean vertical speed (± 1 SD) in m s^{-1} to terminal dive destination depth categories calculated for 36 narwhals tagged between 1993 and 2000. The exponential curve was fit to mean values for each depth category by minimizing sums of squares errors. Note the change of scale on the x-axis

southern wintering ground spent on average over 3 h d^{-1} (SD 0.6) occupying depths >800 m, whereas whales from the northern area only spent 0.7 h (SD 1) at this depth. Note, if maximum dive depths were actually deeper than 800 m, some proportion of occupancy time calculated here would be composed of transit time. For mid-water depths (100 to 400 m), average occupancy time per dive (AOT_{dive}) was not different between the 2 wintering grounds (Table 4). For dives to depths >800 m, AOT_{dive} was twice as long in the southern wintering ground, indicating whales in this area spend more time on each dive occupying deep depths. Round trip transit time was positively correlated with depth and was the same for both wintering grounds. Specifically for the bins of interest to this study, round trip transit time was 5 min (SD 0.3) per dive to 200 m, 8 min (SD 0.2) per dive to 400 m and approximately 13 min (SD 0.5) per dive to >800 m.

DISCUSSION

The selection of different wintering rounds by isolated sub-populations provides the opportunity to contrast the ecology of narwhal foraging in different areas. The overall increasing trend in the number of dives to deep depths follows well with the general pattern reported for narwhals between summer and winter (i.e. increasing dive depths in the fall and the deepest dives occurring in winter). The comparative analysis on the wintering grounds revealed pronounced differences between the 2 sites, which was also indicated by analysis of independent sub-population behavior. Summering site origin appeared to be a more important factor driving in seasonal changes or choices in diving behavior than wintering locality (lower AIC values). Time at temperature data for whales in 2001, in combination with CTD casts, was in exceptional agreement with the results from pressure recording tags on the northern wintering ground. Consequently, the preference for the mid-water section of the water column on the northern wintering ground was consistent between years both in terms of depth and temperature measurements. Narwhals farther south appear to be spending most of their time diving to and occupying deeper depths along the steep slopes of Baffin Bay. The intensity and frequency of these deep dives suggest directed foraging on the bottom.

Monodontids are social creatures that travel in groups and accordingly exhibit similar group behavior. Female and male whales are found in mixed pods, and share the same summering and wintering grounds year round, as well as migratory routes and timing. It is thus justifiable to assume that a sub-sample of narwhals (both males and females) are a representative sample of a sub-population based on: (1) intra-annual similarity in dive behavior early during the tracking period, when tags on all whales were performing well; (2) inter-annual similarity in dive behavior at a single locality; and (3) similarities in diving behavior, depar-

Table 4. *Monodon monoceros*. Dive parameters estimated from the time budget model for individual narwhals in the northern and southern wintering ground. AOT_{day} is average occupancy time per day in the depth category, AOT_{dive} (AOT_{day}/# dives) is average occupancy time per dive in the depth category, and ATT_{dive} (AOT_{dive} plus the round trip transit time for a dive) is average total time for a dive to that depth category. All parameters are expressed in minutes. SD is reported in parentheses

Depth bin (m)	Northern wintering ground			Southern wintering ground		
	AOT _{day}	AOT _{dive}	ATT _{dive}	AOT _{day}	AOT _{dive}	ATT _{dive}
0–50	677 (44)	11 (2)	11 (2)	750 (119)	6 (2)	6 (2)
50–100	30 (25)	4 (1)	6 (1)	39 (28)	5 (2)	7 (2)
100–200	111 (62)	7 (1)	10 (1)	36 (34)	6 (2)	9 (2)
200–400	157 (24)	6 (1)	11 (1)	38 (27)	8 (5)	13 (5)
400–600	64 (14)	6 (1)	13 (1)	45 (45)	8 (4)	17 (3)
600–800	9 (9)	4 (1)	14 (1)	10 (16)	5 (5)	17 (4)
>800	43 (57)	7 (1)	20 (1)	185 (40)	12 (3)	25 (2)

ture dates and movement paths of whales from multiple localities during the same seasons.

Here, inferences to population behavior are made based on a sample of 16 individuals from 3 localities (each sampled for 2 to 3 consecutive years). The satellite tags had different duration periods and individuals were not tracked for the same duration of time, nor was there a representative sample of both sexes during all periods. The lack of evidence suggesting a reduced diving capability in females, together with results from previously published studies demonstrating females are capable of deep dives (Heide-Jørgensen & Dietz 1995), suggest that the dissimilarity in dive behavior on the wintering grounds is not a result of sex-specific diving behavior. When male and female diving behavior was compared from the same summering locality over a period of 80 d, results clearly indicated females were not restricted in the depth of dives or the number of dives to deep depths. In the cases where significant differences were reported between sexes, females made more deep dives than males. Although female narwhals tend to be smaller than males (about 350 vs 400 cm), the physical difference in length or mass does not appear to restrict deep diving ability.

The observations on the number of dives to mid- and deep-water depth categories and the proportion of time spent in those categories may indicate site- or sub-population-specific selective use of the water column. There are several possible explanations for the divergence in behavior, including differences in habitat structure, prey availability or innate adaptations between sub-populations. Whales in the northern wintering ground are spread between the continental shelf and the Baffin Bay abyss (Fig. 1). These narwhals occupy deeper water (significantly deeper than those farther south). The southern wintering ground is more elongated, located precisely along the 1400 m depth contour with a maximum depth recorded for whale locations of 1750 m. Based on the similarity in behavior for multiple narwhals in the area (many dives d^{-1} exceeding 800 m) and the narwhal with the high-resolution tag (50% of dives >800 m exceeded >1400 m), it appears that narwhals rely heavily on foraging on the bottom in this region. Curiously, whales in the deeper northern wintering ground have access to deeper depths, yet make shallower dives. It is possible that whales in the northern wintering ground forage or spend more time in mid-water not because they directly select for shallow depths, but because reaching the bottom is more costly or impossible. Alternatively, if narwhals specifically target mid-water depths, the maximum bottom depth in their range may not be an important factor in their choice of location. The maximum limit of the pressure transducer prevented recording the deepest dive depth; therefore, actual maximum depth remains unknown.

In this study, 3 of the 16 whales were equipped with TDRs for the first few days of tracking (IDs 3964, 7297 and 7928) and estimates of mean ascent and descent rates ranged from 0.6 (SD 0.4) to 1.5 (SD 0.4) $m s^{-1}$ (Laidre et al. 2002). TDR ascent and descent rates were compared to the SLTDR average vertical transit speed for the 2 shallowest bins (where most of the diving occurred when TDRs collected data) and results were in good agreement, indicating the method used here for estimating vertical speed provided results which were consistent with that from an instrument with much higher sampling rate and resolution.

It is likely that not all dives are directed towards specific depths, and foraging time may quite possibly include searching at multiple depths for prey patches. Histogram-structured data potentially mask this and may suggest individuals are not selective in their utilization of the water column if they dive to the bottom in habitats with different bathymetric structure. Parameter estimates describing the number of dives per day or absolute time per day in a depth category are not independent from estimates for other depth categories. In particular, the estimates for each depth category were derived using independent depth-specific models; however, the estimates are not independent from each other. In the case of binned data, the depth category where the number of deep dives peaks is an indication of dive focus, yet the absolute value will vary in different habitats. The modal number of dives on the southern wintering ground (bottom dives) is less than (almost half) that for mid-water dives on the northern wintering ground. This disparity likely arises due to temporal and physiological constraints on diving to deep- versus mid-water depths. Thus, it is likely that the whales decide to make a deep dive at or close to the surface. This hypothesis is also supported by the asymptotic behavior of vertical speeds at deeper depths (Fig. 6).

The vertical distribution of narwhal prey in the water column influences feeding behavior and dive tactics. In summer, narwhals feed sparingly on Arctic cod *Arctogadus glacialis* and Polar cod *Boreogadus saida* at the ice edge, shifting to deep-water prey species such as Greenland halibut or *Gonatus* squid in early fall and winter (Finley & Gibb 1982). Directed foraging on high densities of Greenland halibut requires that narwhals dive to at least 800 m, as surveys for Greenland halibut in the wintering grounds report highest densities between 800 and 1200 m (Treble et al. 2000, 2001, Jørgensen 2002). Based on our model, diving to these depths requires a travel time of 14 to 15 min per dive, allowing no more than 11 min of foraging time per dive for a maximum submergence of 25 to 26 min based on estimates of aerobic dive limits (Schreer & Kovacs 1997, Laidre et al. 2002). Impacts from winter narwhal

predation on Greenland halibut have been detected in Greenland halibut densities and length frequencies, particularly on the southern wintering ground, and numerous full narwhal stomachs have been found in whales harvested in winter, with most containing fresh remains from Greenland halibut (Laidre 2003). In combination with the diving behavior results presented here, it appears that narwhals are intensively feeding during the winter period.

Narwhals in the northern wintering ground may rely more heavily on mid-water species, such as *Gonatus* squid spp. or polar cod. Polar cod are primarily a pelagic species, though they are sometimes associated with the bottom (Jørgensen 2002). *Gonatus* are also common at mid-water depths (found as shallow as 200 to 600 m; Kristensen 1984, Santos et al. 2001), yet also found on the bottom along the continental slope. Diving to pelagic depths of 200 to 600 m requires a shorter travel time of 5 to 9 min per dive with longer foraging time available to whales. Clearly, whales do not select for a single species; however, prevalence and predictable occurrence of prey or differences in habitat structure might influence selection. Regional differences in the spatial and temporal patterns of prey density may shape winter foraging behavior of narwhals.

Studies examining the trade-offs of deep versus shallow diving have defined 3 important factors affecting foraging behavior: (1) energetic cost to the individual; (2) probability of capturing prey; and (3) the relative energetic benefit of the prey. Costa (1988) examined metabolism at sea as a function of dive rate for northern fur seals and found that energy expended during deep or shallow dives was potentially equivalent. Williams et al. (2000) documented gliding as an important behavioral strategy used by marine mammals during deep dives, where lung compression at depth reduced energetic costs by up to 59%. This energy saving feature appears to be a general phenomenon for several species of mammalian divers. If the cost of deep diving is minimal, then foraging behavior is reduced to the probability of capturing prey and how the energetic contribution of the prey fits into total energetic requirements of the predator. Martin & Smith (1999) documented foraging behavior of beluga whales *Delphinapterus leucas* in the Canadian High Arctic and determined that based on dive durations, belugas could spend 50% more time foraging in shallower, coastal water areas than in deeper offshore waters, and concluded that deep-water foraging areas must offer unusually high rates of prey intake and densities.

Overall, our data suggest behavioral differences between the 2 wintering grounds occupied by different sub-populations of narwhals in the Baffin Bay and Davis Strait region. It is not clear if these observed patterns result from responses to local prey availability,

cost-benefit trade-offs or innate differences in behavior between discrete sub-populations. Evidently, spatial and temporal variation in prey abundance exists within the ecosystem, and it seems plausible that a large predator would optimize its foraging strategy to obtain the maximum net gain in an area. There may be significant selective advantages and opportunities for local adaptation associated with consistently returning to a familiar area with predictable resources or environmental conditions. Thus, to a certain extent, narwhal movements, diving and site fidelity may reflect behavioral traits that have proved successful over centuries or larger time scales, although not necessarily optimal in each year. The marked consistency in annual movement patterns and seasonal habitat selection between sub-populations suggests a learned behavior, probably maternally directed and evolutionarily driven. This study reinforces the importance of the wintering grounds to narwhal sub-populations in Canada and Greenland, and provides documentation of behavioral differences supporting preference for separate summering or wintering localities.

Acknowledgements. Tagging projects were funded by the Greenland Institute of Natural Resources, the National Environmental Research Institute (Denmark), the Department of Fisheries and Oceans (Canada), the Nunavut Wildlife Management Board (Canada), the Commission for Scientific Research in Greenland, the Danish Natural Research Council (51-00-0131), and the Danish Environmental Protection Agency (as part of the environmental support program Danish Cooperation for Environment in the Arctic). The National Marine Mammal Laboratory, School of Aquatic and Fishery Sciences (USA), and the Washington Cooperative Fish and Wildlife Research Unit, Biological Resources Division, US Geological Survey provided funding for the analysis. P. R. Richard and J. Orr assisted in the field and office. D. P. DeMaster is gratefully acknowledged for providing travel funding for fieldwork in Canada and Greenland. D. Hoekman organized dive data and, together with M. Kingsley, provided assistance with the vertical speeds. M. Simpkins provided generous assistance with repeated measures models. The manuscript was improved by the comments of 4 anonymous reviewers.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: October 16, 2002; Accepted: July 22, 2003
Proofs received from author(s): September 25, 2003