Differences in dive behaviour among the world's three narwhal *Monodon monoceros* populations correspond with dietary differences

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ABSTRACT: Satellite tracking of animals can provide information on their foraging behaviour, behavioural flexibility, and potential prey. Differences in diet among narwhals *Monodon monoceros* from the Baffin Bay (BB), East Greenland (EG) and Northern Hudson Bay (NHB) populations have been detected using stable isotope analysis. Presumably, differences in diet should correspond to differences in dive behaviour among populations, which we evaluated using satellite-linked tags. Thirty-four narwhals were equipped with transmitters in order to evaluate the total number of dives and time spent in pre-defined depth categories. Repeated-measures ANOVAs found narwhals from EG made significantly more dives and spent more time in the mid-water column compared to other populations. NHB narwhals made more dives in the deep zone than in the mid-water region. BB narwhals spent time and made most dives within the upper water column and the deep zone, which suggests deep-dwelling prey may contribute substantially to their diet. Within the BB and EG populations there were sex-specific differences in time spent at depth and we identified seasonal changes in diving for all populations. This is the first study to compare dive behaviour in all 3 of the world's narwhal populations. We found that dive behaviour differences among populations paralleled differences in diet. Results suggest that narwhals employ specialized foraging strategies, which have repercussions on their potential ability to adapt to ecosystem changes.

KEY WORDS: Narwhal · *Monodon monoceros* · Satellite tracking · Diving behaviour · Time at depth

INTRODUCTION

Satellite tracking of animals indirectly provides information on their foraging habits (Thompson et al. 2003, Jonsen et al. 2007, Varo-Cruz et al. 2013), ecological traits (Wade et al. 2006, Andrews et al. 2008), habitat use (Chilvers 2008), and changes in their habitats (McCafferty et al. 1999, Laidre & Heide-Jørgensen 2007). Satellite tracking is particularly useful for monitoring marine mammals, as they are difficult to observe in their natural environment and often make extensive migrations into inaccessible areas. Although the satellite tracking instruments, as well as the process of instrumenting the animals is costly, for some animals and some environments it is the only feasible approach for monitoring individual behaviour. Satellite tracking instruments can also be equipped with sensors for determining dive depth, and satellite-linked time-depth recorders are commonly used to assess diving ability in marine mammals as they provide binned dive data including maximum dive depths and the fraction of time spent in different depth bins (Laidre et al. 2004, Linnenschmidt et al. 2013). These data provide insight into

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habitat preference, foraging behaviour, and potential prey the animal may be targeting based on presence of prey species at those particular depths.

Narwhals *Monodon monoceros* are Arctic cetaceans, best known for the spiral tusk present in males. The narwhal spends almost half of the year in heavy pack ice and darkness (Laidre & Heide-Jørgensen 2011) and satellite tracking provides a way to monitor their locations and behaviour during this time. Based on previous satellite tracking and genetic analyses, there are 3 defined populations of narwhals in the world (Dietz et al. 2008, Westdal 2009, Petersen et al. 2011). The Baffin Bay (BB) population numbers >60 000 individuals (Richard et al. 2010) and spends summer (approx. June–September) in the fiords and inlets in the Canadian high Arctic and the inlets of Northwest Greenland (Dietz et al. 2008). They then begin their migration of ~1700 km to Davis Strait, where they remain until April before returning to the summering grounds (Watt et al. 2012). There are approx. 12 500 narwhals in the Northern Hudson Bay (NHB) population (Asselin et al. 2012). They spend summer in northwestern Hudson Bay, and then migrate ~1250 km to their wintering grounds in the eastern Hudson Strait (Richard 1991). The East Greenland (EG) population is estimated at approximately 6000 individuals (Heide-Jørgensen et al. 2010). Narwhals from this population have been tracked from their summer residence in fiords and inlets in Scoresby Sound to offshore wintering grounds on the shelf area right outside Scoresby Sound (M. P. Heide-Jørgensen et al. unpubl. data). A small number of narwhals also occur around Svalbard and these narwhals are assumed to be part of the EG population.

Narwhals from the BB population have been satellite tagged previously (n = 98) (Martin et al. 1994, Dietz & Heide-Jørgensen 1995, Heide-Jørgensen & Dietz 1995, Dietz et al. 2001, Heide-Jørgensen et al. 2002, 2003, 2014, Laidre et al. 2002, 2003, 2006, Laidre & Heide-Jørgensen 2007, Dietz et al. 2008, Watt et al. 2012). Narwhals in this population have also been tagged with D-tags (tags that provide acoustic, depth, orientation, and acceleration information) and instrumented with Crittercams, which provided information on dive behaviour (Dietz et al. 2007). However, no information on diving behaviour has been presented for narwhals from the NHB and EG populations. Three juvenile narwhals were tagged near Svalbard, Norway in August 1998 (Lydersen et al. 2007); however, tag duration was maximum 46 d, and therefore more work on narwhals from EG is required. Data on surfacing time for narwhals in NHB, which is useful for correcting visual aerial surveys, have been presented (Westdal 2009, 2013), but no analysis of dives to all depths has been conducted for these whales.

Narwhals are among the Arctic marine mammals most sensitive to climate change, in part because of their limited behavioural flexibility and specialized diet (Laidre et al. 2008). In addition, evaluation of narwhal muscle has shown that these animals have morphological and physiological adaptations that allow them to survive the harsh Arctic winters, but which also limit their behavioural flexibility (Williams et al. 2011). Dive behaviour has only been examined in narwhals from the BB population; thus, no comparisons among populations have been made to determine if populations are flexible in their foraging behaviour, or if different populations have adapted to the varying environmental conditions specific to their region. If differences in narwhal behaviour across populations can be detected, it suggests narwhals may have greater behavioural flexibility than previously believed.

Dietary studies of narwhal stomach contents have only focused on the BB population and have found that diet is composed primarily of Greenland halibut *Reinhardtius hippoglossoides*, Arctic cod *Boreogadus saida*, polar cod *Arctogadus glacialis*, and squid *Gonatus fabricii* (Finley & Gibb 1982, Laidre & Heide-Jørgensen 2005). Dietary studies using stable isotope analysis on narwhals from all 3 populations suggest significantly different diets (Watt et al. 2013). Stable isotope analysis showed that narwhals from EG fed in a more pelagic food web, while narwhals in NHB fed in a more benthic food web, and those from BB fed in both food webs approximately equally (Watt et al. 2013). Within the BB population, diet and food consumption also varies seasonally (Finley & Gibb 1982), which is common for marine mammals living in these seasonally extreme and dynamic environments (Bluhm & Gradinger 2008). Stable isotopes also indicated a seasonal difference in diet for NHB narwhals (Watt & Ferguson 2015); however, nothing is known about seasonal changes in diet for the EG population. Seasonal changes in dive parameters have been noted for the BB population, where an increase in deep dives in the winter has been identified (Laidre et al. 2003); however, these deep dives were not matched with the bottom bathymetry at the dive location to investigate whether the narwhal may have been feeding in the deep-water zone. As a result, further investigation of changes in dive behaviour in all populations, and a comparison of dive behaviour among populations, is warranted, as this would suggest different foraging strategies not yet detected.

Differences in foraging behaviour in males and females have been found in a number of marine mammals (Le Boeuf et al. 2000, Beck et al. 2003, Baird et al. 2005). Narwhals display sexual size dimorphism, where adult males are significantly larger than adult females (Garde 2011). Increased size enhances an individual's ability to dive and stay at depth for longer periods of time (Schreer & Kovacs 1997, Irvine et al. 2000, Noren & Williams 2000, Mori 2002). Due to the size differences, males potentially have the ability to dive longer and deeper than females, and may have an increased dive effort if they have greater energy requirements than non-gravid and non-lactating females (Kleiber 1932). Within the BB population, Heide-Jørgensen & Dietz (1995) found female narwhals had lower dive rates than their male counterparts. However, Laidre et al. (2003) found no differences between the sexes, thus warranting further investigation of dive behaviour between males and females.

The specific objectives of this study were to determine if dive behaviour of animals from the 3 narwhal populations is congruent with what would be expected based on their diet. We hypothesized narwhals from NHB would be more likely to be making dives to the deep zone to feed on prey in this region, those from EG would be mid-water divers were they would be able to forage on pelagic prey, and BB narwhals would make dives to the deep zone as well as some mid-water dive behaviours. In addition, based on bottom bathymetry, we expected the narwhals in the 3 populations to spend a different amount of time diving depending on their geographic location. For instance, narwhals from BB overwinter in Davis Strait, which has depths up to 2000 m, and therefore whales from this population would need to make energetically expensive deep dives and have greater recovery time at the surface, which has been seen for other deep diving animals (Kooyman & Ponganis 1998). Narwhals from EG can experience depths up to 1000 m in their region, but based on results of Watt et al. (2013), which indicated narwhals in this population forage primarily on pelagic prey, we predicted they would be spending more time foraging at mid-depths.

Within each population, we predicted males would make more dives and spend more time at depth because of their greater body size. We also hypothesized that we would identify seasonal changes in dive behaviour that would reflect changes in primary prey and their home range at this time. In BB, Watt & Ferguson (2015) found a seasonal shift in diet and although exact prey responsible for this shift were difficult to distinguish, it appeared that narwhals fed more on pelagic prey in the winter and benthic prey in summer, albeit not significantly. This is counter to other studies that have found that benthic prey, such as Greenland halibut *Reinhardtius hippoglossoides*, is dominant in the winter (Laidre & Heide-Jørgensen 2005). Thus, although we expected a change in dive behaviour, whether this would result in more dives to the deep zone in the winter or summer was difficult to predict for BB narwhals. In NHB, seasonal differences in diet have also been identified, but to a much lesser extent than for narwhals in BB (Watt & Ferguson 2015). As a result, we predicted seasonal shifts in dive behaviour would be less evident for these narwhals. Little is known about seasonal diet or dive behaviour of EG narwhals, but we expected they would also have seasonal differences in dive behaviour related to shifts in diet since they inhabit deep-waters in winter, much like BB narwhals.

MATERIALS AND METHODS

Study areas

Narwhals from the 3 populations were tagged near the communities of Pond Inlet (BB) and Repulse Bay (NHB), Nunavut, Canada, and Ittoqqortoormiit, East Greenland (EG). From the BB population, 3 females and 2 males were tagged in Tremblay Sound (72° 21′ 23″ N, 81° 6′ 24″ W) in August 2010, and 6 females and 1 male were tagged in 2011 (Fig. 1, Table 1). From the NHB population, 2 females and 3 males were tagged in Lyon Inlet (66° 30′ N, 84° 00′ W) in August 2006, and 1 female and 3 males were tagged in Repulse Bay (66° 31′ 19″ N, 86° 14′ 06″ W) in August 2007 (Fig. 1, Table 1). From the EG population, 3 males and 3 females were tagged in 2010, and 6 males and 1 female in were tagged in 2011, at Hjørnedal in Scoresby Sound (70° 39′ 22″ N, 27° 48′ 50″ W) (Fig. 1, Table 1).

Capturing and instrumenting the narwhals

Methods for whale capture and satellite tagging have been previously described (Orr et al. 2001, Dietz et al. 2008). Briefly, narwhals were caught in nets set perpendicular to the shore in waters with a maximum depth of approximately 60 m. Nets were dark green or black in color with 40 × 40 cm mesh and 3.5 to 5 m deep. Nets were anchored to a large stone on shore on one end and attached to a bag of large rocks at the offshore end. Nets were kept afloat using 6 to 8 white buoys (30 cm diam.) that were clearly visible from
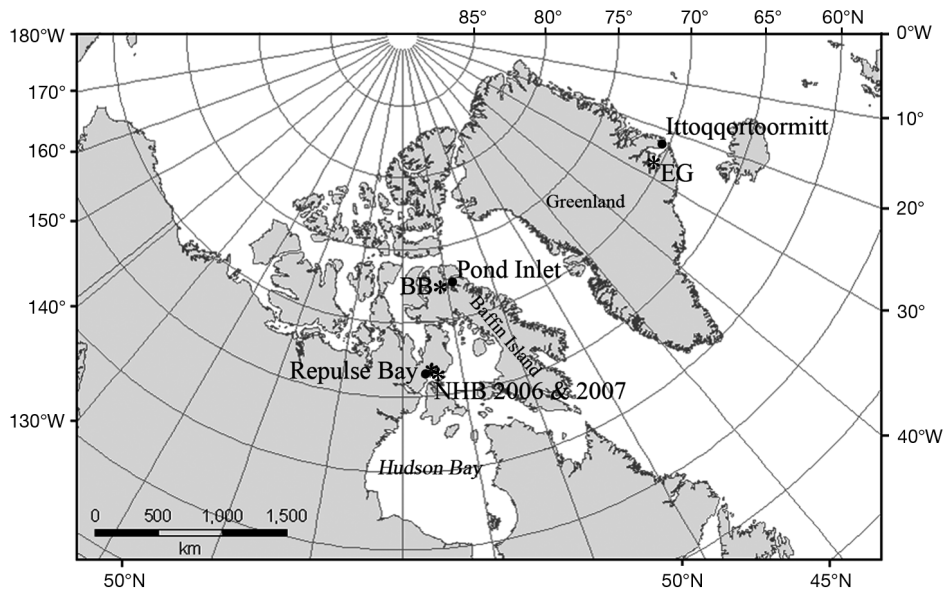
Fig. 1. Tagging sites (∗) and closest communities (●) in Canada and Greenland where narwhals were tagged in East Greenland (EG), Northern Hudson Bay (NHB), and Baffin Bay (BB). Tagging locations differed in 2006 and 2007 for the NHB population as indicated

Table 1. Deployment date, date of last transmission, and total length of transmission period for narwhals deployed with satellite-linked transmitters. Sex and morphometric data are also indicated for each narwhal

Population: Tagging location	Deployment date (yy-mm-dd)	Last transmission (yy-mm-dd)	Transmit length (d)	Sex	Tag no.	Length (m)	Fluke length (m)	Tusk length (m)
NHB: Lyon Inlet	2006-08-11	2007-06-11	305	M	57595	4.37	1.12	1.52
NHB: Lyon Inlet	2006-08-11	2006-12-24	146	M	57597	2.62	0.66	0.27
NHB: Lyon Inlet	2006-08-11	2007-04-20	253	M	57598	3.53	–	0.91
NHB: Lyon Inlet	2006-08-11	2007-04-04	237	F	57599	3.96	0.89	–
NHB: Lyon Inlet	2006-08-11	2007-06-03	297	F	57596	3.96	0.86	–
NHB: Repulse Bay	2007-08-08	2007-11-15	100	F	36641	4.00	0.90	–
NHB: Repulse Bay	2007-08-09	2007-12-09	123	M	40152	3.75	0.89	0.98
NHB: Repulse Bay	2007-08-09	2007-12-17	131	M	37024	3.85	0.92	1.10
NHB: Repulse Bay	2007-08-10	2007-11-22	105	M	40622	3.64	0.91	1.01
BB: Tremblay Sound	2010-08-21	2011-04-28	250	M	51871	4.44	1.07	1.56
BB: Tremblay Sound	2010-08-21	2011-02-10	320	M	51872	4.61	1.03	1.00
BB: Tremblay Sound	2010-08-22	2011-10-10	413	F	51873	4.00	0.90	–
BB: Tremblay Sound	2010-08-22	2011-02-26	187	F	51874	3.90	0.96	–
BB: Tremblay Sound	2010-08-24	2011-01-25	153	F	51875	3.80	0.93	–
BB: Tremblay Sound	2011-08-16	2012-02-23	191	F	51876	3.91	0.85	–
BB: Tremblay Sound	2011-08-16	2011-12-22	129	M	51878	3.10	0.76	0.20
BB: Tremblay Sound	2011-08-16	2012-06-25	314	F	51879	4.01	0.91	–
BB: Tremblay Sound	2011-08-18	2012-03-30	225	F	39314	4.06	0.93	–
BB: Tremblay Sound	2011-08-18	2012-03-07	202	F	39270	3.94	0.97	–
BB: Tremblay Sound	2011-08-19	2011-12-22	126	F	39315	3.89	0.95	–
BB: Tremblay Sound	2011-08-19	2012-01-16	151	F	57590	4.04	1.04	–
EG: Scoresbysund	2010-09-02	2010-12-29	118	M	3960	4.00	1.20	0.90
EG: Scoresbysund	2010-08-22	2011-02-17	179	F	3963	3.95	0.89	–
EG: Scoresbysund	2010-09-02	2011-02-15	166	M	3964	3.85	0.95	1.04
EG: Scoresbysund	2010-09-04	2011-07-12	311	F	6335	3.95	0.95	–
EG: Scoresbysund	2010-09-04	2010-11-13	70	M	93093	2.75	0.69	0.09
EG: Scoresbysund	2010-09-04	2011-06-09	278	F	93094	4.15	0.95	–
EG: Scoresbysund	2011-08-12	2012-03-06	207	F	6336	3.15	0.68	–
EG: Scoresbysund	2011-08-12	2012-01-09	150	M	7926	4.07	1.04	1.00
EG: Scoresbysund	2011-08-12	2012-01-18	159	M	20162	3.92	0.97	0.98
EG: Scoresbysund	2011-08-13	2012-03-03	203	M	93098	2.90	0.72	0.23
EG: Scoresbysund	2011-08-16	2011-10-22	67	M	93095	3.70	0.90	0.83
EG: Scoresbysund	2011-08-19	2012-05-12	267	M	93101	4.53	1.08	1.70
EG: Scoresbysund	2011-08-19	2012-03-18	212	M	10946	3.64	0.80	0.60

shore. The nets were monitored 24 h and narwhal were easily detected in the net as one or several of the buoys would be completely submerged. When this occurred, one zodiac boat with 3 to 4 people on board would drive out to where the buoy had gone down and pull the narwhal(s) to the surface. A second zodiac with 3 to 4 people would drive to the anchor line and cut the net from the anchor. The shore crew (5 to 6 people) would then pull the net into shore. Once close to shore, the narwhal was positioned with its tail in the shallowest water, and disentangled from the net. In Canada, a veterinarian monitored heart rate and condition (e.g. blood samples) throughout the tagging process. The satellite tag was attached with 2 or 3 nylon pins (10 mm length) through the fat and blubber under the dorsal ridge.

Narwhals in Canada were equipped with SPLASH tags (Wildlife Computers) that were programmed to transmit daily during the summer from July 1 to September 31 and subsequently on a 3 d duty cycle. Thus, four 6 h data blocks were programmed to transmit (whether they all transmitted depended on the connection with the tag that day) every day from July to September, and every third day from October to June for the BB and NHB narwhals. Narwhals in Scoresby Sound were equipped with Mk10 transmitters that were on a 2 d duty cycle, where four 6 h data blocks were collected every second day. Although daily transmissions provide more detailed movements of narwhals, the duty cycle allows for a longer deployment period. Data on location of all deployed tags were obtained from the ARGOS system (CLS America). ARGOS data files were extracted using WC-DAP 3.0 Build 69 software (Wildlife Computers). Dive information was grouped into defined depth bins and represented the 6 h time span directly prior to the transmission. Due to the differences in the ocean bathymetry for the different populations, tags were programmed to collect data within different dive depth bins. For the BB population, the number of dives to different depths were binned into 6, 8, 10, 12, 15, 20, 100, 200, 400, 800, 1000, 1400, 1800 and >1800 m bins. Percent of time at each depth was binned into 1, 2, 3, 4, 5, 20, 100, 200, 400, 800, 1000, 1400, 1800, and >1800 m bins. Dives from the NHB population were binned in 6, 8, 10, 12, 15, 20, 25, 50, 100, 200, 300, 400, 500, and >500 m depth bins, and time at depth was binned in 1, 2, 3, 4, 6, 8, 10, 12, 20, 36, 50, 100, 200, and >200 m bins. The tags for EG narwhals were programmed to bin dives into 1, 2, 4, 200, 500, 800, 1100, 1400, 1700, 2000, and >2000 m bins, and time at depth was binned in 0, 2, 4, 200, 500, 800, 1100, 1400, 1700, 2000, and >2000 m bins.

Data analysis

Dive depth and time at depth bins were associated with a location that occurred within the 6 h binned time frame on a particular day. Location information from the tags was categorized based on the accuracy of the transmission, varying from Class A and B, and 0 to 3. Class A and B provide no location information, Class 0 includes an error range of >1500 m, Class 1, 500–1500 m, Class 2, 250–500 m and Class 3, <250 m. Shape files of ocean bathymetry were obtained from IBCAO (international bathymetric chart of the Arctic ocean), which provide 500 m^2 grid files (Jakobsson et al. 2012), and used to estimate a depth for each narwhal location through extraction using a North Pole projection in ArcGIS. Only Class 2 and 3 locations were used in analysis, as they are both within the error range associated with the IBCAO depths. After bathymetry data for each day was obtained, in order to compare across populations because different populations live in areas with vastly different bathymetries (for average depths experienced by each population across seasons see Fig. 2), dives to a particular depth bin were converted into a percent of total depth. Dives were then grouped into depth categories, including dives that occurred in the upper water column (surface = 0–25 % of total depth),
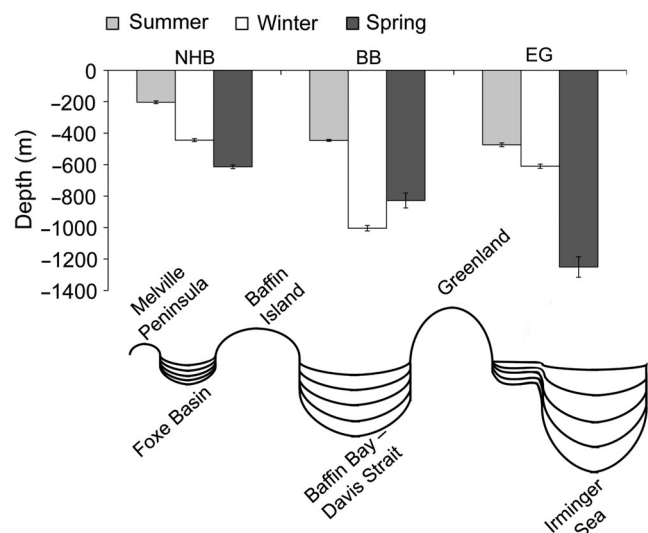

Fig. 2. Mean depth (± SE) available to narwhals in each population across seasons according to depth at satellite location (once every 6 h period). Depth categories were calculated by dividing ocean depth into 4 equal categories (surface, mid-surface, mid-deep, deep; indicated by the 4 lines) at each dive location, which differed according to dive location (indicated by different distances between the lines illustration) and summing the total number of dives or percent of time spent in each of these depth categories. See Fig. 1 for abbreviations

those that occurred in the upper mid-water region (mid-surface = 26–50%), in the lower-mid-water region (mid-deep = 51–75%), and those dives that occurred in the deep zone (deep = 76–100% of the total depth). Dives were often deeper than the IBCAO depths (15.5 ± 2.5%), indicating the uncertainty with the bottom bathymetry at these remote locations; in these cases, these dives were included in the 76–100% category. The same data preparation was done for the time spent at each depth bin in order to determine how much time was spent at the surface, in the mid-surface and mid-deep regions, or in the deep zone, for the BB and EG populations, but not the NHB population. Bathymetric depths never exceeded the tag's programmed depth readings except for the NHB population, where tags were only programmed to >500 m for dive depth and >200 m for time at depth. Dives occurred in the >500 m bin, but this bin was always included in the 75–100% depth category; thus, regardless of whether whales were diving 501 m or 1000 m these dives would have been included in the deep zone. However, for time at depth, a large proportion of time was spent in the >200 m category and 200 m was often not included in the 75–100% depth category. Since we cannot surmise whether these dives should have been included in the mid-surface, mid-deep, or deep zone, it was not possible to interpret the time spent at different depths for narwhals from NHB.

We evaluated the total number of dives and time at depth across populations using a repeated-measures full factorial ANOVA, which considered individuals nested within each population as a random effect, and population (3 levels: BB, NHB, and EG for dive depth; and 2 levels: BB and EG for time at depth), depth (4 levels: surface, mid-surface, mid-deep, and deep), and the interaction between these factors as main effects (Underwood 1997). Normal probability plots were used to assess normality. The assumption of sphericity was tested using the Mauchly criterion (Mauchly 1940) and in instances where the sphericity assumption was violated, the adjusted Greenhouse-Geisser degrees of freedom were used, which multiplies the calculated epsilon by the original degrees of freedom to create a more conservative test that controls for type I error rates (Greenhouse & Geisser 1959). The nested nature of the design accounted for within-subject variability, while depth was considered a repeated-measures factor since number of dives to one depth would impact the number of dives an individual could make to another depth category (i.e. they were not independent) (Underwood 1997). When significant factors were identified, post-hoc

Tukey's HSD tests were used to determine where significant differences occurred.

To investigate if number of dives and time at depth varied between sexes and across seasons for each population, a full factorial repeated-measures ANOVA which considered individuals nested within each sex as a random effect, and sex (2 levels), season (3 levels: winter, summer, or spring), depth (4 levels: surface, mid-surface, mid-deep, and deep) and all possible interactions among the factors, as main effects; Tukey's tests were used for post-hoc comparisons (Underwood 1997). Diving was defined as occurring in summer (June through September), winter (October through March) or spring (April to May) based on previous satellite tracking studies (Dietz et al. 2001) and as defined by Finley & Gibb (1982). Although there were 2 years of satellite tagging for each population, we were unable to include year as a factor in our analysis because the number of males and females tagged per year varied and the length of tag transmission did not always include all seasons, which resulted in insufficient degrees of freedom to evaluate differences between years. All statistics were conducted using JMP 9.0 software.

RESULTS

The repeated-measures ANOVA for number of dives to each depth category revealed there was a significant interaction between population and depth ($F_{4,15962} = 939.05$, $p < 0.0001$). Tukey's HSD tests revealed that narwhals from BB made significantly more dives within the upper water column (surface) than narwhals from NHB or EG ($p < 0.05$), and narwhals from EG made the fewest dives to this zone ($p < 0.05$; Fig. 3). Narwhals from EG had significantly
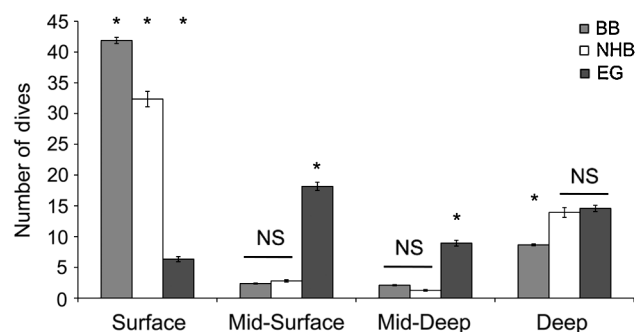
Fig. 3. Mean number of dives (± SE) made to the 4 different depth categories for narwhals from EG (n = 1437), NHB (n = 576), and BB (n = 3540). Asterisks indicate a significant difference, while lines with NS indicate no significant difference among the populations. See Fig. 1 for abbreviations
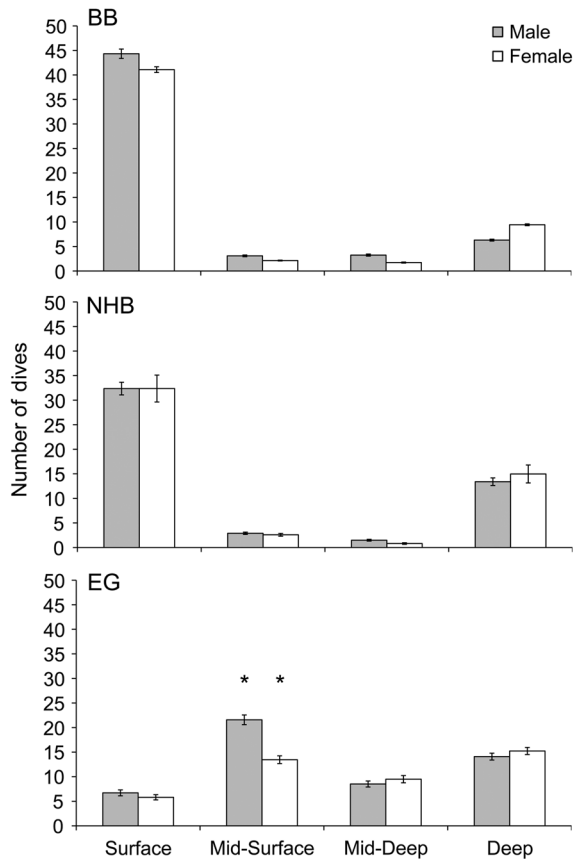
Fig. 4. Mean number of dives (± SE) made to the 4 different depth categories for male and female narwhals from BB (n = 877 and 2663, respectively), NHB (n = 384 and 192, respectively), and EG (n = 832 and 605, respectively). No significant differences between males and females were observed. See Fig. 1 for abbreviations

Fig. 5. Mean number of dives (± SE) made to the 4 different depth categories for narwhals from BB, NHB, and EG during summer (n = 2205, 140, and 450, respectively), winter (n = 1134, 375, and 959, respectively), and spring (n = 201, 61, and 28, respectively). Asterisks indicate a significant difference among seasons, while lines with NS indicate no significant difference among seasons. See Fig. 1 for abbreviations

more dives to the mid-surface and mid-deep depths compared to narwhals from BB and NHB (p < 0.05), who made a similar number of dives to these depths (p > 0.05; Fig. 3). Narwhals from NHB and EG made a similar number of dives to the deep zone (p > 0.05), but made significantly more dives to this depth category than narwhals from BB (p < 0.05; Fig. 3).

Repeated-measures ANOVA investigating the number of dives across seasons and sexes within each population found there was a significant interaction between depth and sex for the BB ($F_{1,5682}$ = 23.64, p < 0.0001) and EG ($F_{3,5034}$ = 13.72, p < 0.0001), but not for NHB ($F_{2,1314}$ = 0.45, p = 0.64). Upon further investigation, although there were significant differences in the total number of dives across the depth categories in BB, within each depth category, males and females made a similar number of dives (p > 0.05; Fig. 4). In EG, male and female narwhals made a similar number of dives in each depth category except in the mid-
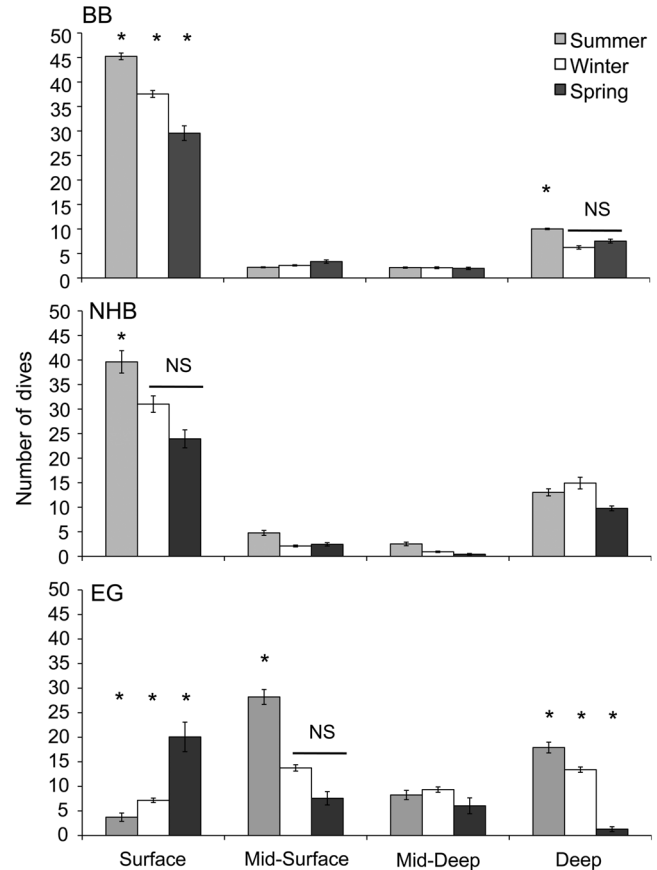
surface zone where males made significantly more dives than females (p < 0.05; Fig. 4). There was also a significant interaction between depth and season in the BB ($F_{2,5682}$ = 40.94, p < 0.0001), EG ($F_{5,5034}$ = 29.69, p < 0.0001) and NHB ($F_{3,1314}$ = 4.60, p < 0.01) populations for the number of dives. In BB, narwhals made significantly more dives in the upper water column during the summer, compared to winter and spring (p < 0.05; Fig. 5). The number of dives made to the mid-water columns did not differ among seasons (p > 0.05), while the number of dives to the deep zone was significantly higher in summer compared to winter (p < 0.05; Fig. 5). In BB, the number of dives targeting the deep zone made in the spring did not differ significantly from winter or summer (p > 0.05; Fig. 5). In NHB, the number of surface dives was significantly greater in the summer compared to winter or spring (p < 0.05); however, there were no significant differ-
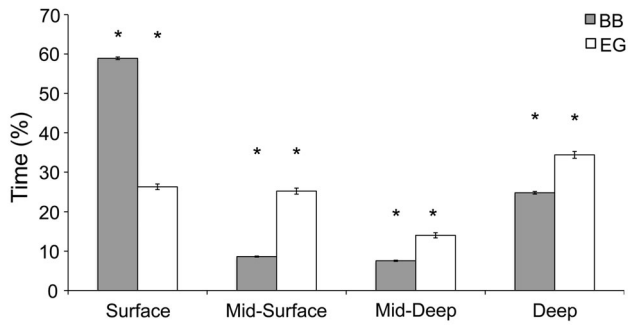
Fig. 6. Mean percent of time spent (± SE) in the 4 different depth categories for narwhals from EG (n = 1440), and BB (n = 3542). Asterisks indicate a significant difference. See Fig. 1 for abbreviations

ences in any other depth category for the different seasons (p > 0.05; Fig. 5). In EG, narwhals made more dives in the upper water column in spring and the least number of dives in summer p < 0.05; Fig. 5). Narwhals in EG made significantly more dives to the mid-surface zone in summer (p < 0.05), and a similar number of dives to the mid-deep category in all seasons (p > 0.05; Fig. 5). Dives targeting the deep zone were more frequent in the summer compared to spring or winter (p < 0.05; Fig. 5).

The repeated-measures ANOVA for time spent in each depth category comparing the BB and EG populations revealed there was a significant interaction between population and depth ($F_{2,15593}$ = 1497.52, p < 0.0001). Tukey's HSD tests showed that narwhals from BB spent significantly more time in the surface depth category than narwhals from EG (p < 0.05; Fig. 6). Narwhals from EG spent significantly more time in the mid-surface, mid-deep, and deep zone compared to narwhals from BB (p < 0.05; Fig. 6).

Repeated-measures ANOVA investigating the total time spent at different depths across seasons and between sexes within the BB and EG populations found there was a significant interaction between depth and sex for BB ($F_{2,7975}$ = 129.16, p < 0.0001), and EG ($F_{3,4715}$ = 27.41, p < 0.0001) narwhals. Tukey's tests revealed that for the BB population males spent significantly more time at the surface than females (p < 0.05; Fig. 7), and for both the EG and BB population, females spent significantly more time in the deep zone than males (p < 0.05; Fig. 7). The model also found a significant interaction between season and depth for BB ($F_{3,7975}$ = 52.63, p < 0.0001), and EG ($F_{6,4711}$ = 15.02, p < 0.0001) narwhals. Narwhals from the BB population spent statistically more time at the surface in winter compared to spring and summer (p < 0.05; Fig. 8). In spring and winter BB narwhals
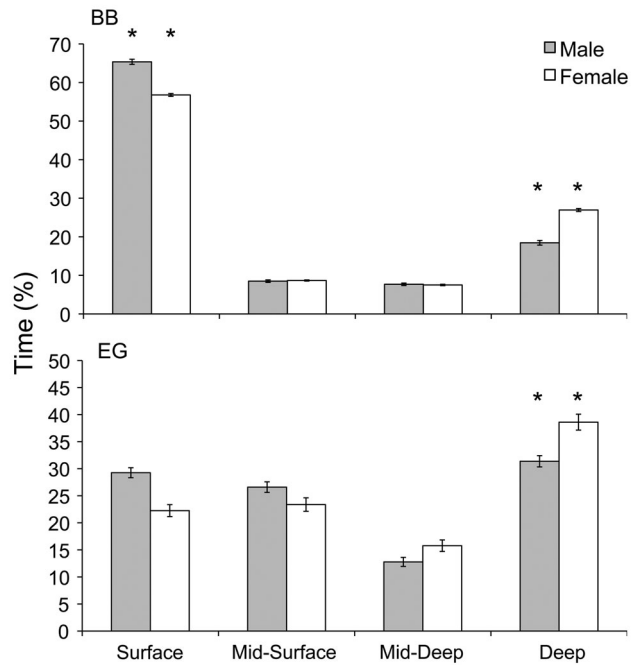

Fig. 7. Mean percent of time spent (± SE) in the 4 different depth categories for male and female narwhals from BB (n = 880 and 2662, respectively), and EG (n = 841 and 599, respectively). Asterisks indicate a significant difference between sexes. See Fig. 1 for abbreviations
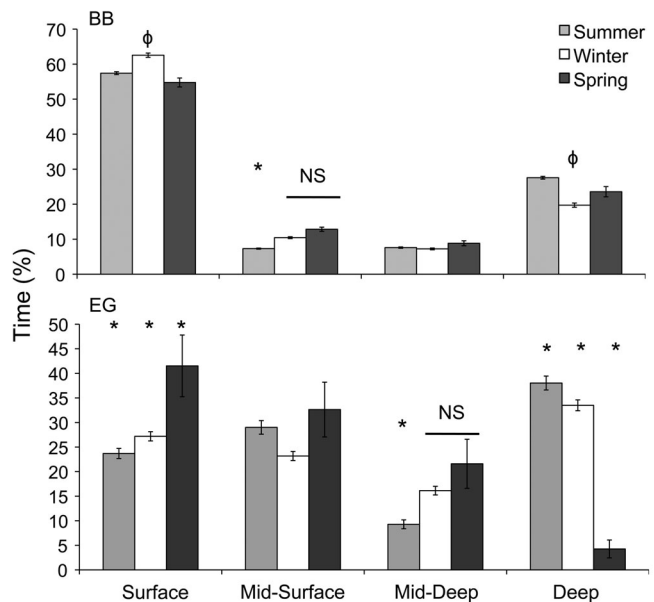

Fig. 8. Mean percent of time spent (± SE) in the 4 different depth categories for narwhals from BB, and EG during summer (n = 2212 and 466, respectively), winter (n = 1131 and 945, respectively), and spring (n = 199 and 29, respectively). Asterisks indicate a significant difference among seasons, lines with NS indicate no significant difference among seasons, and phi (φ) indicates a significant difference between winter and the other seasons, but no significant difference between summer and spring. See Fig. 1 for abbreviations

spent significantly more time at the mid-surface depth than in summer (p < 0.05; Fig. 8). Time spent in the deep zone was significantly less in winter compared to spring and summer for narwhals in BB (p < 0.05; Fig. 8). In EG, narwhals spent significantly more time at the surface in spring and the least amount of time in summer (p < 0.05; Fig. 8). There was no significant difference in the time spent in the mid-surface zone across seasons (p > 0.05), but significantly less time was spent in the mid-deep zone in summer compared to the other seasons (p < 0.05; Fig. 8). Significantly more time was spent in the deep zone in the summer, and the least time was spent at this depth in the spring for narwhals from EG (p < 0.05; Fig. 8).

DISCUSSION

According to stable isotope biomarkers, narwhals from the 3 different populations foraged differently. In particular, there was evidence that narwhals from EG foraged in a more pelagic food web, narwhals from NHB ate more benthic prey, and those from BB foraged approximately equally in both food webs (Watt et al. 2013). Narwhals from NHB and EG had dive behaviour that reflected what would be expected based on these dietary conclusions. For instance, narwhals from EG made significantly more dives to the mid-water zone than narwhals from the other populations, and spent more time there than narwhals from the BB population, which suggests this may be an important foraging area for these whales. Narwhals from EG also spent a significant amount of time in the deep zone, suggesting they must also be foraging here, although to a lesser extent than in the mid-water column where their dietary signature is primarily constituted. NHB narwhals made more dives to the deep zone than the mid-water regions and made a number of surface dives. Marine mammals are limited in their foraging time because they can only hold their breath for a physiologically imposed period before needing to return to the surface to breathe. Dives to the deep zone offer greater opportunities for encountering and capturing prey; however, time at the surface to recover increases rapidly with dive length for many species (Kooyman & Ponganis 1998). Unfortunately, we were unable to evaluate time at the surface for NHB narwhals, but given that they made a significant number of dives in the upper water column, we would also have expected them to spend ample time at the surface since they may need to recover from dives to the deep zone.

We hypothesized that narwhals from BB which forage in benthic and pelagic food webs approximately equally would spend similar amounts of time in the mid and deep zones, but we actually observed that BB narwhals made more dives to the deep zone and spent the vast majority of their time at the surface. If BB narwhals are diving extremely deep, which has been noted previously (Laidre et al. 2003), they need to spend more time at the surface recovering from these dives, which may explain why most of their time is spent in this part of the water column. We predicted they should also be spending a significant proportion of their time in the mid-water regions since dietary studies show they also forage in this zone to a large extent (Watt et al. 2013); however, they spent less time in the mid-water regions (~15%) compared to the deep zone (~25%). It is possible we are overlooking some mid-water foraging that is occurring on the journey to or from the depths, or narwhals could be foraging on prey that are found very deep, but are still pelagic in nature since our deep-water zone included dives that occurred anywhere from 75 to 100% of total possible depth and they may have been foraging in the upper portion of this range. Pelagic prey, including Arctic cod and capelin *Mallotus villosus* are known to make diel migrations (Benoit et al. 2010), and may travel deeper into the water column to evade predators; therefore, narwhals may need to dive to the deep zone to forage on these seasonally pelagic prey. This is also true for some benthic prey, such as Greenland halibut, that are typically found in the benthos but are capable of making vertical migrations (Boje et al. 2014).

We were unable to detect differences in the number of dives made between males and females to the deep zone in any population. Adult males could potentially make more dives to greater depths than females because of their larger body size (Garde et al. 2007). We may not have captured this difference because the males and females tagged were of similar body size; the average size of captured males in EG was 3.7 m while females were 3.8 m, in BB, males averaged 4.1 m and females were 4.0 m, and on average the size of tagged females in NHB was greater than that of males (4.0 m compared to 3.6 m). Asymptotic body length for female narwhals from the BB population is approximately 4.0 m, while males are estimated at 4.6 m (Garde et al. 2007). The fact that population-wide male and female body size was not captured in our small tagged sample may have limited our ability to detect differences in dive performance between males and females; however, other studies of narwhal dive behaviour have also been

unable to identify differences in total dive number between males and females (Laidre et al. 2003) and previous dietary studies have not found strong differences in diet between the sexes (Watt et al. 2013, Watt & Ferguson 2015).

Despite showing little difference in the number of dives to different zones, there was a significant difference in the time males and females spent at depth; females actually spent a greater amount of time in the deep zone than males in the BB and EG populations, counter to what we predicted based on body size. This has also been seen in grey seals *Halichoerus grypus*, where males spend less time at the bottom compared to females (Beck et al. 2003). Beck et al. (2003) suggested this could be a result of larger males being more efficient foragers than females because their larger size may allow them to capture and handle prey more efficiently or they may be less selective foragers and spend less time in search for prey. In addition, smaller animals may be able to dive longer because they rely more heavily on anaerobic respiration (Mori 2002), although there is currently no evidence of anaerobic metabolism in narwhals. In our study, tagged males and females were of similar size, thus size-related efficiency could not explain females spending a greater amount of time at depth than males. Another possibility, specific to male narwhals, may be that the tusk aids in foraging (Dietz et al. 2007) and thus make males more efficient foragers and able to spend less time at depths searching and handling prey. A greater sample size with more equitable representation of both sexes would help clarify these hypotheses.

Seasonal differences in the dive behaviour of narwhals from BB have been identified previously (Laidre et al. 2003) and it appears that the other 2 narwhal populations also exhibit changes in their dive behaviour across seasons. Laidre et al. (2003) found that for narwhals in the BB population, the number of dives to deep depths and the time spent at depth increased in the winter. In contrast, when we factored in bottom bathymetry and evaluated number of dives and time spent in the deep zone for narwhals tagged in BB, dive rate and time in this zone was actually significantly higher in the summer, when they are in shallow waters, compared to winter when they are in deeper waters. Laidre & Heide-Jørgensen (2005) suggested that narwhals conduct a minimal amount of foraging in summer and gain most of their energy in the winter months. However, studies of seasonal changes in body condition of narwhal are limited by sample size and temporal coverage. For example, based on 158 samples collected over 3 months (July to September), Hay (1984) suggested postnatal narwhals forage in summer because female and male body condition increased throughout the season (Hay 1984), whereas Finley & Gibb (1982) used 73 samples collected over 4 months (June to September) to suggest condition decreases in females (possibly because of greater demands imposed by lactation), with no change in males throughout the summer. Typically it is assumed that dives to deep depths, which are relatively energetically expensive, are related to foraging. Based on stable isotopes, Watt et al. (2013) found BB narwhals were consuming slightly more benthic prey in summer than winter, which would result in more dives to the deep zone at this time of the year, and is congruent with our results. However, if it is assumed that narwhals gain most of their energy in the winter and are not foraging in the deep zone in summer, there must be another reason for making dives to this depth zone during summer. Narwhals may be evading disturbances on the surface, or they could be utilizing the rough bottom surface as a means for molting and sloughing off skin. This has been shown in the narwhal's closest relative, the beluga whale *Delphinapterus leucas* (St. Aubin et al. 1990), but has never been documented for narwhals. More research on the potential benefits of diving in the summer, whether it is for molting or foraging, is needed to elucidate the reasons for increased diving to the deep zone during the summer in BB narwhals. In BB, winter and spring diving did not differ across the depth categories except for in the surface category, where narwhals made more dives and spent more time at the surface in the winter compared to spring. This may be a result of seasonal changes in sea ice; narwhals may need to spend more time navigating heavy pack ice for leads and cracks in the ice in the winter (Laidre & Heide-Jørgensen 2011), compared to the spring when the ice is breaking up and access to air is greater.

Diving behaviour of narwhals in the EG and NHB populations, not previously studied, also differed in dive parameters with season. The NHB narwhals live in a shallow habitat in the summer, and unlike the BB narwhals who migrate to the Davis Strait reaching depths over 1500 m in the winter, they migrate just outside the Hudson Strait and rarely experience depths greater than 700 m. Likely as a result of this, they showed relatively little variability in the number of dives to different depth categories across seasons. The EG population did display variation in dive behaviour across seasons and showed a similar pattern to the BB population, with dives to the deep zone and

time in the deep zone being greatest in the summer when in shallower water. This may indicate summer foraging on deep-zone prey; however, stomachs analyzed in the summer have been primarily empty (Heide-Jørgensen et al. 2014) and narwhals from EG have a dietary signature significantly influenced by pelagic prey (Watt et al. 2013). If their dietary signature is not being influenced much by bottom-dwelling prey, it again suggests other advantages to deep-zone diving in the summer months that require further evaluation. Narwhals from EG spend more time in the upper water column in spring and winter, and a similar amount of time in the mid-surface region in these seasons, suggesting this may be an important time for foraging since their dietary signature is primarily influenced by pelagic prey (Watt et al. 2013). Since there were almost no dives to the deep zone in spring, this may also be an important period for migration and horizontal movement, with little time for diving and vertical movements.

Satellite tagging has the ability to provide location information as well as information on dive parameters that would otherwise not be possible for some animals. However, there are limitations with this method of data collection. GIS locations can be off by kilometers. In addition, we only have 4 locations (if conditions are favorable) per day or every 3 days in some seasons, and the collected dive information represents only a 6 h window directly before the transmission. Aside from the limitations of the Argos locations, the bottom bathymetry of this region has also not been mapped in detail. We used IBCAO to assign a bottom bathymetry to each location. Bathymetries are largely based on ship tracking sounds with interpolation between soundings, and in the Arctic shipping traffic is limited (although it is beginning to increase) and thus many data points are interpolated (Jakobsson et al. 2012). However, we believe this is currently the most accurate method for assigning depths to locations and it is more useful to compare populations in relation to their habitat rather than to compare absolute values without considering the spatial structuring of their marine environment. These estimates can only improve as our understanding of the Arctic and research in the Arctic progresses.

The results of this study suggest that narwhals from different populations have different dive behaviours, spending variable amounts of time within the depth categories in their respective habitats, and therefore are perhaps more behaviourally flexible than previously believed. Future studies should investigate muscle tissue of narwhals from all populations to determine if this morphological adaptation for living in extreme environments (Williams et al. 2011) is dependent upon the geographic location of the populations and their corresponding dive behaviours. This is the first study to evaluate dive behaviour in the NHB and EG narwhal populations, and it is the first to investigate differences in dive behaviour among populations. Results were generally in accordance with what would be predicted based on dietary studies using stable isotopes (Watt et al. 2013) and highlight the behavioural differences in narwhals that are adapted to living in different habitats and foraging on different prey. An increased number of narwhals tagged from all 3 narwhal populations is required to assess annual or decadal changes in behaviour that cannot be assessed in the current study. Sex differences may also become apparent with a greater proportion of whales tagged, females in particular. Furthermore, differences in dive behaviour between females with calves and those without may reveal a greater distinction between male and female dive behaviour since females with calves may have to balance limiting their deep zone diving because of the aerobic capabilities of their young, while still foraging enough to support lactation costs. Future satellite tagging studies should continue to monitor changes in dive behaviour that may coincide with changes in foraging behaviour or ice availability and quality. In conclusion, the world's 3 narwhal populations use different parts of the water column, target different prey and may be less specialized foragers than previously believed. In addition, it appears that investigating diet through chemical techniques such as stable isotopes (Watt et al. 2013) can provide congruent information and inform predictions of dive behaviour for marine organisms.

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