RESEARCH ARTICLE

K. L. Laidre · M. P. Heide-Jørgensen · M. L. Logdson
R. C. Hobbs · P. Heagerty · R. Dietz · O. A. Jørgensen
M. A. Treble

Seasonal narwhal habitat associations in the high Arctic

Abstract Movements and behavior of top marine predators are often closely linked with productive oceanic fronts or regional prey aggregations. Consequently, it is of interest to quantify habitat needs and preferences, which can facilitate predictions of conditions favoring persistence and success. Multivariate habitat models of movements and dive behavior of narwhals (*Monodon monoceros*, Linnaeus) in the eastern Canadian high Arctic and West Greenland were developed using data collected from satellite telemetry studies on three separate sub-populations. Twenty-six narwhals were captured between 1993 and 2000 and fitted with satellite-linked time–depth recorders. Geographic positions of whales at 24-h time steps were linked to dive behavior variables compressed on a daily scale, including numbers of dives to different target depths or durations, time near the surface, daily dive rate, and travel speed. Whale movements and behavior were linked to biophysical variables in a raster format using a GIS (bathymetry, bottom topography, bottom temperature, and distance from the coastline) and analyzed using linear and generalized linear mixed models, accounting for temporal autocorrelation and random variation among individuals. Models suggested that several physical variables described narwhal behavior, predominantly bathymetry and distance from the coastline (particularly deep or long dives). Other descriptor variables, such as size category and sex, also explained portions of the model variability, particularly for shallow dives, surface time, and dive rates. Bottom temperature (°C) was the strongest predictor of all dive behaviors when narwhal location data were restricted to periods with available temperatures. The bottom temperature range and gradient selected by narwhals on their wintering grounds often coincided with areas of concurrent high density of Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) and predictable open water in winter pack ice in Baffin Bay. These quantitative habitat models made it possible to reconcile the behavioral traits of narwhals with dynamic environmental factors.

K. L. Laidre (✉)
School of Aquatic and Fishery Sciences,
University of Washington, Box 355020, Seattle,
WA 98195, USA
E-mail: Kristin.Laidre@noaa.gov
Fax: +1-206-5266615

M. P. Heide-Jørgensen
Greenland Institute of Natural Resources, Box 570,
3900 Nuuk, Greenland, Denmark

M. L. Logdson
College of Ocean and Fishery Sciences,
University of Washington, Box 355351,
Seattle, WA 98195, USA

K. L. Laidre · R. C. Hobbs
National Marine Mammal Laboratory, AFSC,
7600 Sand Point Way NE, Seattle, WA 98115, USA

P. Heagerty
Department of Biostatistics, University of Washington,
Box 357232, Seattle, WA 98195, USA

R. Dietz
Department of Arctic Environment,
National Environmental Research Institute,
Frederiksborgvej 399, Box 358, 4000 Roskilde,
Denmark

O. A. Jørgensen
Danish Institute for Fisheries Research, Charlottenlund Slot,
2920 Charlottenlund, Denmark

M. A. Treble
Canada Department of Fisheries and Oceans,
Central Arctic Region, Freshwater Institute Science Laboratory,
501 University Crescent, Winnipeg, MB, RT3 2N6, Canada

Introduction

Patterns of resource use and habitat preference are consequences of behavioral selection constrained by seasonal access, migration patterns, and life-history strategies. Resource use is typically elucidated by

characterizing classes or categories of "habitat", a suite of resources within spatial and temporal proximity. Terrestrial and marine mammals often choose habitats that offer the greatest fitness, and consequently habitat utilization is often assumed to reflect the quality and abundance of resources in an area (Boyce and McDonald 1999; Carroll et al. 1999, 2003; Gregr and Trites 2001). In most cases, habitats are not readily available to a population at all times and exclusion from preferred areas may be due to temporal or physical constraints (Arthur et al. 1996; Matthiopoulos 2003). In addition, habitat selection is inevitably dynamic, as habitat choice is determined by variables that are themselves in flux. Quantifying habitat selection ideally should require knowledge of both an individual's location in space and time and a measure of the individual's activity (i.e. foraging, resting, searching) (Kareiva and Wennergren 1995; Macdonald and Rushton 2003).

In the marine ecosystem, habitat selection studies are complicated by infrequent observations of species at the surface, the inability to observe and document behavior in the water column, and an environment that is highly dynamic and difficult to characterize. Top marine predators often integrate variability in ecosystem productivity (Boyd et al. 2002) and can be used to make broad-scale conclusions about oceanographic features that most strongly influence distribution and abundance. Some kinds of recurrent oceanographic processes aggregate prey and create high-quality, predictable forage sites, which attract predators (Becker and Beissinger 2003). Consequently, it is of great interest to quantify the relationship between marine habitat features and habitat use of apex predators for greater insight into the "marine landscape" and the fundamental processes characterizing important foraging regions.

In the three-dimensional marine environment, one of the few ways of deriving behavioral metrics is by remote telemetry. One of the most common telemetry devices used on marine mammals is the satellite-linked time–depth recorder (SLTDR). These instruments provide both multiple daily geographic positions (based on Doppler shift of received signals when individuals are at the surface) and binned dive data, recording dive depths, dive durations, and time at depth summarized in four 6-h periods (e.g. Heide-Jørgensen and Dietz 1995; Burns and Castellini 1998; Folkow and Blix 1999; Frost et al. 2001; Laidre et al. 2003; Loughlin et al. 2003). Relating predator behavior to spatial location and area use derived from tagging studies shows great promise for habitat-selection studies in the marine environment (Barber et al. 2001; Boyd et al. 2002; Lea and Dubroca 2003).

Throughout their migrations, Arctic cetaceans, such as the narwhal, integrate a large range of habitats over an annual cycle. Narwhals migrate in the fall from high Arctic summering grounds to lower Arctic wintering grounds, the spatial and temporal patterns of which are tightly linked to the cyclical seasonal changes in Arctic waters (Dietz et al. 2001; Heide-Jørgensen et al. 2002, 2003). Narwhals return to their summering site by migrating north in the spring (Heide-Jørgensen et al. 2003), traversing > 3,000 km. In this study, SLTDRs were deployed on narwhals in high Arctic Canada and West Greenland between 1993 and 2000 and movements and diving behavior were monitored for up to 7 months. Results were used to fit multivariate spatial and temporal habitat-selection models to tagging data based on simultaneous quantification of movements, dive behavior, and geo-referenced habitat parameters.

Materials and methods

Capture and instrumentation

Data from 26 narwhals (*Monodon monoceros*, Linnaeus) captured between 1993 and 2000 were used in the analysis (Table 1). Whales were tagged in 1993–1994 in Melville Bay, West Greenland (Melville Bay summering sub-population) ($n=8$), in 1997–1999 in Tremblay Sound, Canada (Eclipse Sound summering sub-population) ($n=11$), and in 2000 in Creswell Bay, Canada (Somerset Island summering sub-population) ($n=7$) (Fig. 1). Narwhals were caught using nets set perpendicular to the shoreline (details described in Dietz et al. 2001). SLTDRs manufactured by Telonics (Mesa, Arizona) and Seimac (Canada) were programmed and cast in epoxy by Wildlife Computers (Redmond, Washing-

Table 1 *Monodon monoceros*. Individual narwhals captured and satellite-tagged in this study. Longevity represents the period of time the whale was tracked with the satellite-linked time–depth recorder. Days of the year are continuous across day 365 for an individual's time series

Locality	ID–year	Longevity (day of the year)	Sex/Size (cm)
Melville Bay	3960–93	245–332	M/ > 400
	3961–93	235–274	M/400
	3962–93	246–276	M/450
	6335–93	240–280	F/400
	20162–93	244–266	M/400
	20688–94	238–260	F/310
	20167–94	239–343	M/405
	20690–94	237–275	F/400
Eclipse Sound	3964–97	236–248	M/370
	6335–97	236–312	M/440
	3961–98	238–308	M/500
	20162–98	234–396	M/475
	20696–98	238–286	F/380
	3964–99	233–450	M/410
	20168–99	224–300	M/410
	20687–99	226–294	F/390
	20688–99	227–311	F/402
	20689–99	227–355	F/405
	20691–99	233–277	F/350
Somerset Island	7927–00	227–324	F/390
	7928–00	227–296	F/370
	20683–00	230–300	F/390
	20688–00	230–348	F/402
	20689–00	230–333	F/397
	20690–00	232–317	F/398
	20691–00	232–245	F/400

Fig. 1 *Monodon monoceros.*
Map of study area showing
summering localities, wintering
areas, and seasonal locations of
narwhals obtained from
satellite tagging studies
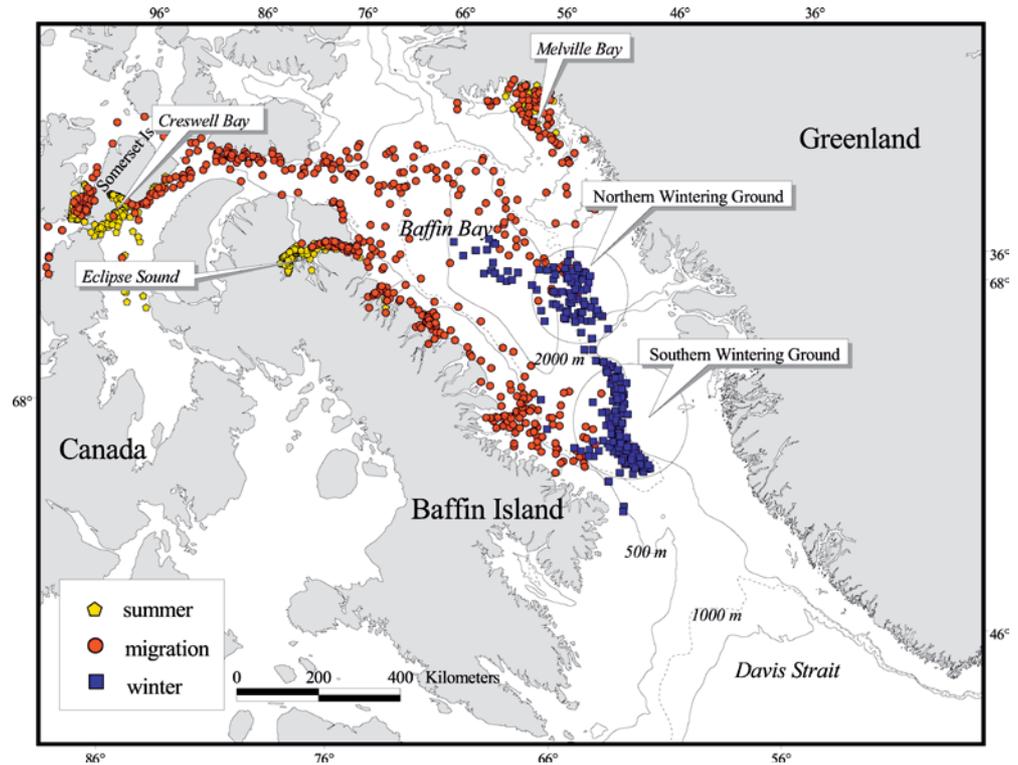
ton) with approximately 0.5 W power output. Transmitters were attached to females on the dorsal ridge with two or three 5–8 mm polyethylene pins. Transmitters were attached to the tusk of males using two stainless steel bands (Seimac SSC3 or the Telonics ST-6 transmitter unit programmed and cast by Wildlife Computers). Sex and standard body length (cm) were recorded for each whale and individuals were classified into one of four size categories: < 375 cm = 1, 375–424 cm = 2, 425–474 cm = 3, ≥475 cm = 4). Transmitter longevity was variable, and consequently individuals were not tracked for the same duration of time.

Satellite telemetry data

Positions and dive data from each individual were assigned to a particular week of the year, month, and one of three seasons: summer (tagging date to 15 September), migration (16 September to 31 October), and winter (1 November to end of tag transmissions), following seasonal movements documented for narwhal sub-populations. Narwhals were assigned to both a summer and winter sub-population region. Whales from summering regions of Melville Bay and Eclipse Sound inhabited a southern wintering ground (SWG) and whales from the summering region of Somerset Island inhabited a northern wintering ground (NWG). A single daily Argos position of high quality (location class 1–3) was selected for each whale during the peak satellite passage (1500 hours local time). The temporal interval between each daily position was ~24 h (SD 2 h). Dis-

tance from the coastline was calculated to examine coordination among individuals from the three sub-populations across years based on 24-h spaced consecutive positions and elapsed time.

All days with complete records of four 6-h period histogram dive data were selected and used to create six summary dive variables on a 24-h scale. Six-hour periods were used to determine the average behavior for three of these parameters using binned dive data: the average total number of dives of < 400 m in a 24-h period, the average total number of dives of > 900 m in a 24-h period, and the average total number of dives of > 24 min duration in a 24-h period. Three additional dive variables (not derived from binned dive data) were the percent of time spent near the surface (≤ 8 m), the daily dive rate (no. of dives h^{-1} of > 8 m), and the daily travel distance. Averages for a 24-h period were composed of the average of available 6-h periods multiplied by 4. All dive parameters were linked with the corresponding daily geographic position for each individual. Daily average total number of dives < 400 m were assumed to indicate the use of surface and mid-water depths relative to habitat features, indicating traveling or shallow foraging behavior. Daily average total number of dives > 900 m were examined to elucidate the frequency of benthic foraging dives at the deepest depth that could be recorded by the satellite tag. Daily average total number of dives > 24 min in duration were used to examine prolonged dives indicating intensive search behavior or deep dives. Daily dive rate and surface time, though not indicating depth selection, indexed the use of surface waters and frequency of departure from them.

Finally, daily travel distance indexed individual speed on a 24-h scale.

Spatial analyses and habitat data

The study area ranged east across Baffin Bay and Davis Strait to the west coast of Greenland starting at 77°N and 100°W with a southernmost point of approximately 66°N. The chosen standard projection was polar stereographic (in meters), with a central meridian of 95°W and a reference latitude of 75°N. Coastline data for Canada and Greenland were obtained from the U.S. Defense mapping agency as part of the World Vector Shoreline (WVS) at a scale of 1:250,000, referenced to mean high water in a datum of WGS84.

Spatial bathymetric data were obtained from the International Bathymetry Chart of the Arctic Ocean (IBCAO, managed by the National Geophysical Data Center). The 2-km continuous variable depth grid was re-sampled to 500-m resolution using local polynomial interpolation in spatial analyses software ESRI Arc-INFO 8.3. A categorical variable depth grid was also created with three depth categories: 0–500 m (shelf), 500–1,500 m (slope), and 1,500–2,300 m (deep). Seafloor slope was calculated as an integer value of the percent rise between adjacent bathymetry grid cells and classified into one of four categories, as follows: 0%, 1–2%, 3–4%, and ≥5%.

Point samples of bottom temperature ($n = 331$) were obtained during random otter trawl surveys for Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) conducted in Baffin Bay and Davis Strait between 16 September and 15 November 1999 and 2001 aboard the R.V. "Paamiut". An average latitude and longitude for each temperature and Greenland halibut catch were used based on the start and end points of each tow. Depths of tows ranged from 290 to 1,482 m. A surface of continuous bottom temperature in Baffin Bay was built using a spherical ordinary kriging model (ESRI Geostatistical Analyst Extension). The continuous bottom temperature grid (ranging from 0.2°C to 4.5°C) was classified into nine categories.

Compiled location and dive data from each narwhal were imported into ArcINFO. The daily positions and dive data metrics were gridded into a raster format at a cell resolution of 500×500 m, selected such that for a given individual, one daily position occupied one pixel. A focal area ("focal" defined as a 40-km diameter circular buffer) was designated around each location corresponding to the average daily travel distance across all seasons. Mean, minimum, and maximum bathymetric depth values were extracted within the focal area around each whale location. Locations for each individual at each time step were spatially associated with categorical slope (percent rise), depth (m), and bottom temperature (°C) variables in ArcINFO. The nearest straight-line distance to the mainland coastline from each daily position was calculated in kilometers.

Statistical analyses

Predictive multivariate habitat models were developed to quantitatively describe narwhal dive behavior for each spatial location at each time step based on a suite of predictor variables taken from the GIS-based analysis of environmental data or information about whale physical features and population structure. Mixed models appropriate for longitudinal data were built for each dependent diving variable. Mixed models accounted for temporal autocorrelation in the data and allowed for a random effect to characterize individual variability in diving behavior among whales. Dependent variables that met the assumption of a normal distribution (dive rate, surface time, travel distance, dives < 400 m) were analyzed with the linear mixed effects procedure fit with maximum-likelihood methods (LME) in S-PLUS version 6.1 (Insightful). Dependent variables measuring non-normal counts of the number of dives > 900 m or > 24 min in duration were analyzed with generalized linear mixed effects models estimated using penalized Quasi-likelihood (GLMM-PQL) based on a Poisson (log link) model structure (Breslow and Clayton 1993). Several spatial autocorrelation structures were explored (with and without a nugget), and temporal autocorrelation between days was ultimately modeled using a spherical spatial autocorrelation structure with a nugget, which provided the best fit to the data as determined by the lowest Akaike's information criteria (AIC) value in the full model. Individual whales were subjects in the autocorrelation models.

For each dependent variable, the best model describing a given dive parameter in space and time was determined using a forward stepwise procedure, where main fixed effects were added to the model from the pool of potential independent variables based on the lowest (AIC) value. Thus the most significant variables entered the model first. Main effects were continuously added at each stepwise increment until the AIC of the model no longer decreased. For GLMMs, the AIC value is approximate since likelihood evaluation is computationally difficult. No interactions were explored. Bottom temperature, only available for positions of whales after 15 October (288th day of the year) in each sample year, was examined as a contributor to the prediction using a subset of location and dive data corresponding to the dates when temperature was available. This excluded movement and dive data from mid-August through 14 October in each year.

Results

Numbers of dives

Variation in the daily average number of dives < 400 m met assumptions of normality due to a large daily sample size for each narwhal (*Monodon monoceros*) and was examined with respect to the predictor variables in

a linear mixed effects model. The subset of dives < 400 m contained 1,281 records of positions from 19 individuals. Average number of daily dives < 400 m was explained by categorical depth, distance from the coastline, size category, and sex (Table 2). Dives < 400 m occurred [on average 149 day^{-1} (SE 31)] with approximately the same frequency on the shelf (0–500 m) and over deep waters (1,500–2,300 m). Dives < 400 m declined with increasing distance from the coast. Dives < 400 m were most commonly made by individuals in size class 3 or female narwhals, categories which were likely correlated. Dives < 400 m were autocorrelated for a period of time as long as 36 days. Whale-to-whale variation accounted for 14% of the total error variance in the model.

The average number of daily dives > 900 m did not meet assumptions of normality due to a large number of zero values and was examined with respect to the series of predictor variables using a generalized linear mixed effects model appropriate for count data. The average number of dives > 900 m, analyzed based on 1,281 records, was negatively correlated with focal mean depth and slightly positively correlated with focal minimum depth. Dives > 900 m increased with increasing distance from the coast (Table 3), corresponding to greater depths, and was not found to be related to any other population parameters. Whale-to-whale variation accounted for approximately 43% of the total error variance in the model.

Duration of dives

The average number of daily dives > 24 min did not meet assumptions of normality due to many zero values and was examined with respect to the series of predictor variables in a generalized linear mixed effects model appropriate for count data. The average number of dives > 24 min was analyzed based on 1,184 records from 19 individuals. This parameter was best explained by focal minimum depth, distance from the coast, and wintering ground location (Table 4). Prolonged dives increased with increasing focal depth and increasing distance from the coast. Prolonged dives were also more frequent on the SWG. Whale-to-whale variation explained 53% of the total error variance in this model.

Dive rate

The average daily dive rate (no. of dives h^{-1} of > 8 m) met assumptions of normality and was examined with respect to the predictor variables in a linear mixed effects model. The daily dive rate contained 1,315 records from 22 individuals. Dive rate was highly dependent on focal mean depth and categorical depth. An average dive rate [7.8 dives h^{-1} (SE 1.02) for a size category 1 narwhal] was negatively related to focal mean depth. Dive rate was also dependent on size category. Whales in size category 3 made at least 2.4 more dives h^{-1} than whales

Table 2 *Monodon monoceros*. Linear mixed effects model: parameters for the average number of dives day^{-1} < 400 m (*AIC* Akaike's information criteria)

Fixed effect	Average no. of dives day^{-1} of < 400 m	SE	df	t-value	P-value	Model AIC
Intercept	149.20	30.80	1,281	4.84	< 0.0001	
Categorical depth						14,040.18
0–500 m	0					
500–1,500 m	−10.34	4.28	1,281	−2.42	0.016	
1,500–2,300 m	2.79	8.75	1,281	0.32	0.750	
Distance from coast	−0.14	0.07	1,281	−2.08	0.037	14,037.63
Size category						14,036.31
Cat. 1 (< 375 cm)	0					
Cat. 2 (375–424 cm)	−16.11	26.32	19	−0.61	0.548	
Cat. 3 (425–474 cm)	90.11	38.90	19	2.32	0.032	
Cat. 4 (> 475 cm)	6.66	38.84	19	0.17	0.866	
Sex						14,035.85
M	0					
F	36.87	23.04	19	1.60	0.126	

Table 3 *Monodon monoceros*. Generalized linear mixed effects model: parameters for the average number of dives day^{-1} > 900 m (*AIC* Akaike's information criteria)

Fixed effect	Log average no. of dives day^{-1} of > 900 m	SE	df	t-value	P-value	Model AIC
Intercept	−1.83	0.38	1,281	−4.77	< 0.0001	
Focal mean depth	0.002	0.0001	1,281	11.34	< 0.0001	5,853.80
Focal minimum depth	−0.0007	0.0001	1,281	−5.84	< 0.0001	5,830.71
Distance to coast	0.005	0.0007	1,281	7.65	< 0.0001	5,826.21

Table 4 *Monodon monoceros*. Generalized linear mixed effects model: parameters for the average number of dives day^{-1} with duration >24 min (*AIC* Akaike's information criteria; *NWG* northern wintering ground; *SWG* southern wintering ground)

Fixed effect	Log average no. of dives day^{-1} of >24 min	SE	*df*	*t*-value	*P*-value	Model AIC
Intercept	−4.29	0.69	1,184	−6.23	<0.0001	
Focal minimum depth	0.0004	0.00009	1,184	4.88	<0.0001	5,891.76
Distance to coast	0.01	0.0006	1,184	17.69	<0.0001	5,841.92
Wintering ground						
NWG	0					
SWG	2.77	0.79	19	3.49	0.0024	5,807.92

Table 5 *Monodon monoceros*. Linear mixed effects model: parameters for the average daily dive rate (dives h^{-1} >8 m)

Fixed effect	Average no. of dives h^{-1} of >8 m	SE	*df*	*t*-value	*P*-value	Model AIC
Intercept	7.79	1.02	1,315	7.64	<0.0001	
Focal mean depth	−0.0007	0.0003	1,315	−2.29	0.022	5,423.85
Categorical depth	−0.13	0.17	1,315	−0.76	0.445	5,421.27
Size category						5,419.11
Cat. 1 (<375 cm)	0					
Cat. 2 (375–424 cm)	−0.57	1.12	22	−0.51	0.614	
Cat. 3 (425–474 cm)	2.45	1.33	22	1.85	0.078	
Cat. 4 (>475 cm)	−0.42	1.45	22	−0.29	0.773	

Table 6 *Monodon monoceros*. Linear mixed effects model: parameters for the average percent of time spent near the surface (<8 m) each day

Fixed effect	Average percent of surface time	SE	*df*	*t*-value	*P*-value	Model AIC
Intercept	42.88	4.59	1,224	9.34	<0.0001	
Focal maximum depth	−0.003	0.001	1,224	−3.10	0.002	9,274.01
Season						9,249.96
Summer	5.65	1.26	1,224	4.49	<0.0001	
Winter	−6.15	1.83	1,224	−3.36	0.0008	
Migration	0					
Size category						9,243.82
Cat. 1 (<375 cm)	0					
Cat. 2 (375–424 cm)	5.57	4.93	22	1.13	0.271	
Cat. 3 (425–474 cm)	−9.36	5.80	22	−1.61	0.121	
Cat. 4 (>475 cm)	8.99	6.48	22	1.39	0.179	

in other size categories (Table 5). Dive rate behavior was correlated for an extended period, up to ~36 days. Whale-to-whale variation accounted for 25% of the total error variance in the model.

Surface time

The average daily surface time met assumptions of normality and was examined with respect to the predictor variables in a linear mixed effects model. The estimates of surface time contained 1,224 records from 22 whales analyzed using a linear mixed effects model. Important predictor variables in the model were focal maximum depth, season, and size category. There was an inverse relationship between focal maximum depth and time spent at the surface (Table 6). Surface time had a clear seasonal component, highest in the summer (~48%) and lowest in the winter (~36%), with an intercept value for migration of 43% (SE 4.6). There were large differences in surface time within each size category, with the least amount of time spent at the surface by whales in category 3. Surface time behavior was correlated up to ~12 days. Whale-to-whale variation accounted for 30% of the total error variance in the model.

Daily travel distance

Whales from discrete sub-populations displayed coordinated movements, both within a year and across several years. Whales tagged within a year moved together with highly synchronized spatial and temporal patterns, and whales tagged in subsequent years at the same site

Fig. 2 *Monodon monoceros.* Distance to coastline (km) from each individual's geographic position (based on a 20-day moving average). Individuals constitute separate lines and are shown in three colors for each sub-population (*blue* Eclipse Sound 1997–1999; *green* Melville Bay 1993–1994; *orange* Somerset Island 2000). Note high degree of coordination between movements of individuals within a sub-population and across years. All movements offshore occurred within a 1–2 week period
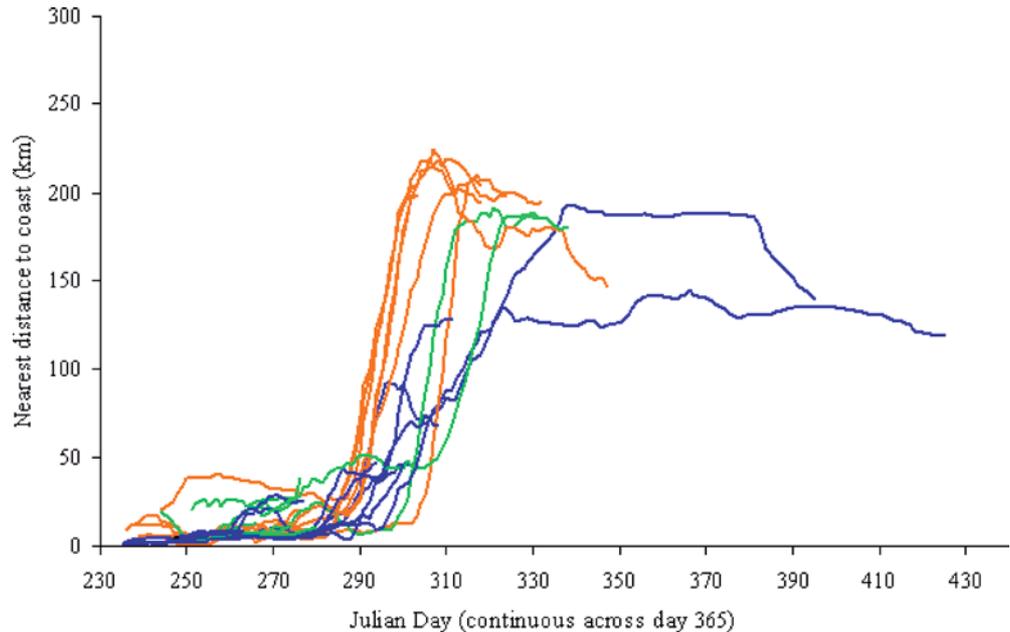
showed remarkable similarity in movements to the previous year. Whales from different sub-populations moved 100–200 km offshore within days of each other, often on the same day, with only two individuals deviating from this pattern in 7 years (Fig. 2). No other behavioral variable in this study showed such coordination or similarity among individuals. The multivariate habitat model for daily travel distance (LME model) was relatively insensitive to the pool of predictor variables, and many variables ($n = 8$) entered the model, accounting for some portion of the variance. Correlation between measurements of daily travel distance for whales was low (1.7 days) and whale-to-whale variation was < 1%.

Models with bottom temperature

Bottom temperature was the most important variable in all models explaining the variance in behavior when narwhal movement and dive data were sub-divided to include only days after 15 October (Fig. 3). In these models, the introduction of bottom temperature displaced all bathymetry predictors. Lower bottom temperatures resulted in increasing dive rate, increased number of dives < 400 m, increased number of dives > 900 m, increased number of dives > 24 min, and decreased surface time. The spatial location of narwhal wintering grounds corresponded to a sharp temperature gradient along the slopes on the east side of Baffin Bay, where temperatures rise from 0°C at 2,000 m to 4.5°C on the shelf. Whale locations were concentrated in a bottom temperature range between 0°C and 1.5°C (Fig. 3). During surveys for Greenland halibut in Baffin Bay in 1999 and 2001, the highest densities occurred in bottom temperatures < 1.5°C (Fig. 4).

Discussion

This study utilized movements and dive data from narwhals (*Monodon monoceros*) instrumented with SLTDRs in conjunction with available environmental data to quantify spatial and temporal changes in habitat selection. Such an associative approach can isolate predictor variables for different behaviors based on generalized habitat features. It is important to keep in mind that large mobile animals, such as narwhals, often show considerable spatio-temporal variation in distribution and behavior and may traverse several habitats within a day (Macdonald and Rushton 2003). Additionally, narwhal behavioral patterns and area use are to some extent determined by evolution, experience, and the inherent site-fidelity of a sub-population. Nevertheless, a modeling approach linking geographic movements, behavior, and the environment over space and time offers a method for relating biological processes to the dynamics of a population and to conservation issues.

Multivariate models that seek linear or non-linear combinations of environmental factors correlated with species presence or behavior provide valid explanations of habitat associations, however, often fail to take into account the possibility that either the environment or behavior may be autocorrelated. Temporal autocorrelation in dive behavior parameters and movement measurements is often stronger than spatial autocorrelation in a species whose behavior is strongly linked to seasonal cycles. Temporal autocorrelation was addressed in the present study by modeling it as a spatial variable in time. The temporal autocorrelation parameters in the models suggest behavior was autocorrelated for periods of < 2 days to > 1 month, depending on the dive parameter of interest.

Fig. 3 *Monodon monoceros.* Bottom temperature (°C) in Baffin Bay and Davis Strait with location of narwhal wintering grounds and depth contours. Note temperature gradient on east side of Baffin Bay
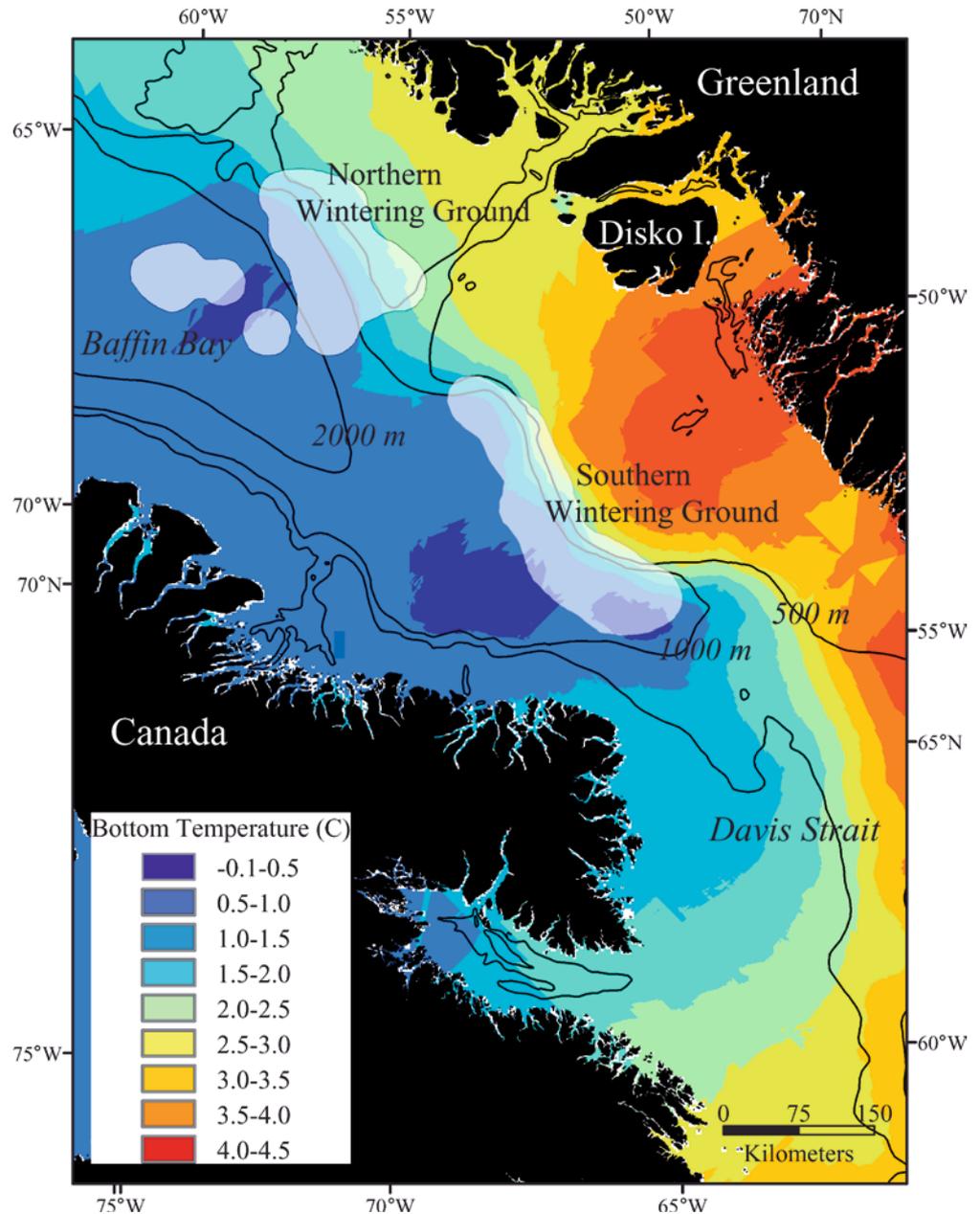
Not all behavioral metrics are closely related to the environment and accordingly may not be easily explained in habitat models. The highly synchronized movements demonstrated by narwhal positions and speed, relative to distance from the coastline, indicate sub-population movements are coordinated and generalizations about resource selection from a sample of tagged individuals can be extended to the population level. The insensitivity of the daily travel distance model results from this observed coordination (also emphasized by the very small whale-to-whale variation contributing to the total error variance) and does not appear to be linked to spatial habitat variables or underlying oceanographic processes. This synchronized behavior is only poorly represented by distance from shore and is likely due to innate migration timing or group-based behavior, following well with other analyses of narwhal movement metrics (Laidre et al. 2004a).

Models for narwhal behavioral variables were universally dependent on some environmental parameter or set of parameters, although some behaviors were also dependent on physiological or population parameters. Both prolonged (>24 min) and deep (>900 m) dives were only dependent on the environment or habitat attributes, including continuous or categorical depth and distance from the coast. The dependence of deep or prolonged dives on depth is not surprising as this behavior is most commonly observed far offshore in waters >1,500 m deep. Dives >900 m were negatively correlated with focal mean depth and slightly positively
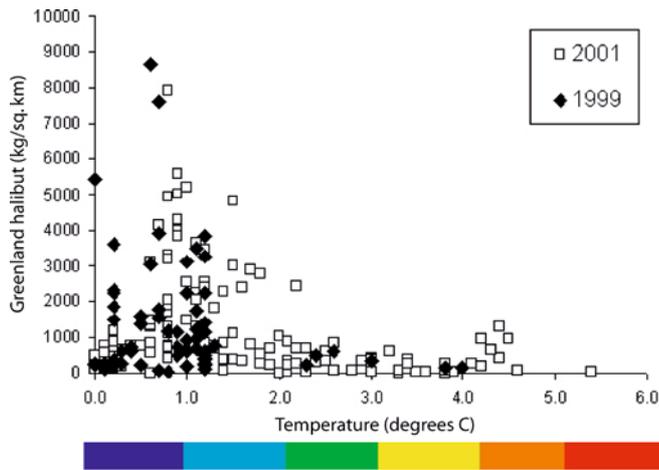
Fig. 4 *Monodon monoceros*. Catches (kg km^{-2}) of Greenland halibut in Baffin Bay in 1999 and 2001, with recorded bottom temperature at time of tow. Note catches peak at 0.5–1.0°C, similar to the bottom temperatures found in the narwhal wintering grounds (see Fig. 3)

correlated with focal minimum depth. This suggests that although focal mean depth explains most of the variance some portion can be explained by focal minimum depth. It is possible whales have more time to search for prey in shallower water where the bottom is reached more quickly. A greater frequency of prolonged dives (>24 min) occurred on the SWG, which correlates closely with evidence of greater benthic predation in this region (Laidre et al. 2003, 2004b). Other behavioral metrics such as dives <400 m, surfacing time, and dive rate were also dependent on parameters such as size category and sex.

Top predators are thought to congregate at predictable sites in response to elevated availability of prey resources driven by physical oceanographic processes (Guinet et al. 2001; Boyd et al. 2002; Becker and Beissinger 2003; Thompson et al. 2003). It is not simple to isolate a single variable affecting prey aggregations or predator fidelity because marine trophic interactions are complex and interwoven. In addition many important variables are not sampled accurately and consistently. Therefore, physical habitat features such as depth or bottom temperature are often used by necessity as proxys for the distribution of prey resources, as was the case in this study.

Models developed on the date-restricted data set to incorporate bottom temperature estimates in Baffin Bay suggested that bottom temperature was the strongest predictor of fall and winter movements and dive behavior of narwhals. Bottom temperature displays an interesting pattern in Baffin Bay and Davis Strait. Temperatures are cold and highly uniform on the west side of Baffin Bay, none are >1.0°C. East of the Baffin Bay abyss towards the West Greenland coast, bottom temperatures display a steep warming gradient across the slope and towards the shelf, increasing from 1.0°C to 2.5°C between 500 and 2,000 m. On the east side of the

shelf, bottom temperatures are much warmer than on the west side, as much as 4.0–4.5°C. The temperature pattern is driven by the influx of North Atlantic water moving along the west coast of Greenland creating a biologically productive zone utilized by sea birds and marine mammals over most of the year (Heide-Jørgensen and Laidre 2004).

The highly significant effect of bottom temperature suggests that this variable is important for choice of wintering areas, or may be a proxy for something not explored in this study. Selection of areas with high gradients in bottom temperatures is likely related to two things: (1) predictable open water in the pack ice where bottom temperatures increase on the east side of Baffin Bay, or (2) areas of higher production in areas with steep bottom temperature gradients influencing benthic prey. Available data indicate narwhals rely heavily on wintering areas in Baffin Bay for at least 6 months of intensive foraging (Laidre 2003; Laidre et al. 2004b). The behavioral effects of increasing bottom temperature (a lower dive rate, fewer dives to all depths, decreased dive durations, and more time at the surface) are consistent with less intensive foraging or searching behavior.

Greenland halibut are widely distributed in the Northwest Atlantic and are found from the Davis Strait northward into Baffin Bay. The main spawning area is believed to be in the Davis Strait, south of 64°N, at depths >1,200 m. Larvae are carried north, and young fish settle on the slope of the banks southwest of Disko Island, Greenland, in water no deeper than 400 m and then migrate to Baffin Bay or coastal deep-water fjords as they grow into adults (Riget and Boje 1989; Jørgensen 1997). Because of this recruitment pattern, Greenland halibut tend to concentrate on either the cool steep slopes offshore in Baffin Bay or in the coastal fjords of West Greenland. Narwhals from West Greenland and the Canadian high Arctic, which have a sympatric distribution with the deep-water Greenland halibut resources in Baffin Bay (Dietz et al. 2001; Heide-Jørgensen et al. 2002; Treble and Bowering 2002), show concentrated diving behavior within the depth range of high Greenland halibut densities and appear to impact halibut length frequencies and densities in their overwintering areas (Laidre et al. 2003, 2004b).

Several sources indicate Greenland halibut distribution is affected by temperature, although densities in different temperature regimes vary by region (Chumakov 1969; Bowering and Brodie 1991; Jørgensen 1998; Bowering and Nedreaas 2000). In the present study, high densities of Greenland halibut were most common in cool bottom temperatures (0.5–1.5°C). Across the entire North Atlantic, Bowering and Nedreaas (2000) reported the highest and most stable catches in temperatures between 0°C and 5.0°C, although catches decline in bottom temperatures >4.0°C. Trends in the Northeast Atlantic are clearer, where catches peak at 1.1–2.0°C and beyond which the average weight per set declines. Jørgensen (1998) reported highest catches of Greenland

halibut in Baffin Bay in 1987–1995 at 1°C or between 3°C and 4°C. Fishing captains in Baffin Bay have recently targeted specific temperature ranges (cold regimes at 1–2°C or warm regimes at 4–6°C) for optimal catches (M. Treble, personal communication). These reports on Greenland halibut correlate well with the cool bottom temperature regimes in the location of the narwhal wintering grounds.

Greenland halibut also occur on the west side of Baffin Bay (uniformly low bottom temperatures), where narwhals do not overwinter. In this area, Greenland halibut appear to occur in higher densities than in whale wintering areas, which has been attributed to lack of predation (Laidre et al. 2004b). Narwhals have been observed returning to the same wintering areas each year and do not alter where they winter based on the highest densities of Greenland halibut. This suggests that narwhal winter habitat choice is not exclusively dependent on high prey densities. More likely, narwhal success is dependent on available open water in dense pack ice. The warmer bottom temperatures due to the influx of North Atlantic water also influence sea ice structure off West Greenland and create more predictable and larger spaces of open water. The importance of bottom temperature may be a proxy for wintertime open water, as it does not appear to correlate directly with whale habitat choice based solely on prey densities.

Narwhal movements and habitat choice may reflect behavioral traits that have evolved over centuries or larger time scales. Site fidelity may be a heritable trait, which, for a sub-population, reflects collective experiences relative to a once reliable resource that may no longer be available. Consequently, not all behavior may be explained by using quantitative habitat models of current conditions. In the case of the narwhal, the narrow habitat choice combined with a limited prey base and clear foraging seasonality makes for a highly adapted species, which is indeed vulnerable to changes in climate and/or habitat variability.

References

Arthur SM, Manly BF, McDonald LL, Garner GW (1996) Assessing habitat selection when availability changes. Ecology 77:215–227

Barber DG, Saczuk E, Richard PR (2001) Examination of beluga–habitat relationships through the use of telemetry and a geographic information system. Arctic 54:305–316

Becker BH, Beissinger SR (2003) Scale-dependent habitat selection by a nearshore seabird, the marbled murrelet, in a highly dynamic upwelling system. Mar Ecol Prog Ser 256:243–255

Bowering WR, Brodie WB (1991) Distribution of commercial flatfishes in the Newfoundland–Labrador region of the Canadian Northwest Atlantic and changes in certain biological parameters since exploitation. J Sea Res 27:407–422

Bowering WR, Nedreaas KH (2000) A comparison of Greenland halibut (*Reinhardtius hippoglossoides*) fisheries and distribution in the Northwest and Northeast Atlantic. Sarsia 85:61–76

Boyce MS, McDonald LL (1999) Relating populations to habitats using resource selection functions. Trends Ecol Evol 14:268–272

Boyd IL, Staniland IJ, Martin AR (2002) Distribution of foraging by female Antarctic fur seals. Mar Ecol Prog Ser 242:285–294

Breslow NE, Clayton DG (1993) Approximate inference in generalized linear mixed models. J Am Stat Assoc 8:9–25

Burns JM, Castellini MA (1998) Dive data from satellite tags and time depth recorders: a comparison in Weddell seal pups. Mar Mamm Sci 14:750–764

Carroll C, Zielinski WJ, Noss RF (1999) Using presence–absence data to build and test spatial habitat models for the fisher in the Klamath region, USA. Conserv Biol 13:1344–1359

Carroll C, Phillips MK, Schumaker NH, Smith DW (2003) Impacts of landscape change on wolf restoration success: planning a reintroduction program based on static and dynamic spatial models. Conserv Biol 17:536–548

Chumakov (1969) The Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)) in the Iceland area—the halibut fisheries and tagging. J Ichthyol 9:900–912

Dietz R, Heide-Jørgensen MP, Richard PR, Aquarone M (2001) Summer and fall movements of narwhals (*Monodon monoceros*) from northeastern Baffin Island towards northern Davis Strait. Arctic 54:244–261

Folkow LP, Blix AS (1999) Diving behavior of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian Seas. Polar Biol 22:61–74

Frost KJ, Simpkins MA, Lowry LF (2001) Diving behavior of subadult and adult harbor seals in Prince William Sound, Alaska. Mar Mamm Sci 17:813–834

Gregr EJ, Trites AW (2001) Predictions of critical habitat for five whale species in the waters of coastal British Columbia. Can J Fish Aquat Sci 58:1265–1285

Guinet C, Dubroca L, Lea MA, Goldsworthy S, Cherel Y, Duhamel G, Bonadona F, Donnay J-P (2001) Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. Mar Ecol Prog Ser 219:251–264

Heide-Jørgensen MP, Dietz R (1995) Some characteristics of narwhal, *Monodon monoceros*, diving behavior in Baffin Bay. Can J Zool 73:2120–2132

Heide-Jørgensen MP, Laidre KL (2004) Declining open water refugia for top predators in Baffin Bay and adjacent waters. Ambio (in press)

Heide-Jørgensen MP, Dietz R, Laidre KL, Richard P (2002) Autumn movements, home range and winter density of narwhals (*Monodon monoceros*) from Tremblay Sound, Baffin Island. Polar Biol 25:331–341

Heide-Jørgensen MP, Dietz R, Laidre KL, Richard P, Orr J, Schmidt HC (2003) The migratory habits of narwhals. Can J Zool 81:1298–1305

Jørgensen OA (1997) Movement patterns of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum) in West Greenland as inferred from trawl survey distribution and size data. J Northwest Atl Fish Sci 21:23–37

Jørgensen OA (1998) Results of the Joint Japan–Greenland Trawl surveys at West Greenland 1987–1995 on Greenland halibut (*Reinhardtius hippoglossoides*) and roundnose grenadier (*Coryphaenoides rupestris*). NAFO (Northwest Atl Fish Organ) Sci Counc Stud 31:21–56

Kareiva P, Wennergren U (1995) Connecting landscape patterns to ecosystem and population processes. Nature 373:299–302

Laidre KL (2003) Space use patterns of narwhals in the high Arctic. PhD dissertation, University of Washington, Seattle

Laidre KL, Heide-Jørgensen MP, Dietz R, Hobbs RC, Jørgensen OA (2003) Deep-diving by narwhals, *Monodon monoceros*: differences in foraging behavior between wintering areas? Mar Ecol Prog Ser 261:269–281

Laidre KL, Heide-Jørgensen MP, Logsdon ML, Hobbs RC, Dietz R, VanBlaricom GR (2004a) Fractal analysis of narwhal space use patterns. Zoology 107:3–11

Laidre KL, Heide-Jørgensen MP, Jørgensen OA, Treble MA (2004b) Deep ocean predation by a high Arctic cetacean. ICES J Mar Sci 61:430–440

Lea M-A, Dubroca L (2003) Fine-scale linkages between the diving behavior of Antarctic fur seals and oceanographic features in the southern Indian Ocean. ICES J Mar Sci 60:990–1002

Loughlin TR, Sterling JT, Merrick RL, Sease JL, York AE (2003) Diving behavior of immature Steller sea lions (*Eumetopias jubatus*). Fish Bull (Wash DC) 101:566–582

Macdonald DW, Rushton S (2003) Modelling space use and dispersal of mammals in real landscapes: a tool for conservation. J Biogeogr 30:607–620

Matthiopoulos J (2003) The use of space by animals as a function of accessibility and preference. Ecol Model 159:239–268

Riget F, Boje J (1989) Fishery and some biological aspects of Greenland halibut (*Reinhardtius hippoglossoides*) in West Greenland waters. Northwest Atl Fish Organ Sci Counc Stud 13:41–52

Thompson D, Moss SEW, Lovell P (2003) Foraging behaviour of South American fur seals *Arctocephalus australis*: extracting fine scale foraging behaviour from satellite tracks. Mar Ecol Prog Ser 260:285–296

Treble MA, Bowering R (2002) The Greenland halibut (*Reinhardtius hippoglossoides*) fishery in NAFO Division 0A. Northwest Atl Fish Organ SCR Doc 02/46:1–10