Space use patterns of narwhals (*Monodon monoceros*) in the high Arctic

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Abstract

SPACE USE PATTERNS OF NARWHALS (*MONODON MONOCEROS*) IN THE HIGH ARCTIC

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Movements and diving behavior of narwhals (*Monodon monoceros*) were examined using satellite-linked time depth recorders deployed on three sub-populations in Canada and West Greenland. Spatial models were used to link satellite telemetry to static and dynamic environmental parameters and elucidate foraging behavior, seasonal ecological relationships, and vulnerability to climate change. Linear mixed effect models, examining time allocation and dive depths during a 5-month winter period, revealed significant differences between whales occupying two distinct wintering grounds in Baffin Bay. Narwhals occupying a northern wintering ground spent most of their time between 200-400 m (25 dives/day, SE 3) and narwhals in a southern wintering ground spent most of their time at depths >800 m (16 dives/day, SE 1). The spatial overlap between narwhal wintering grounds (95% kernel area use) and the abundance and biomass of Greenland halibut (*Reinhardtius hippoglossoides*) suggested lower halibut densities and skewed length frequencies in areas occupied by narwhals. Evidence of heavy predation during the winter period followed well with stomach contents examined from narwhals taken during a winter harvest and predicted prey consumption estimated by a bioenergetic model. Increasing trends in sea ice were detected in wintering grounds in Baffin Bay, suggesting a reduced amount of open water available to whales and potential for lethal ice entrapments. Daily locations were linked to bottom depth, slope, distance from the coast, and bottom temperature and movement paths were quantified using the fractal measure of complexity. Strong seasonal habitat selection was apparent and results suggested possible local variation between the wintering grounds. The use of location and diving data collected from satellite telemetry provided sufficient information for a detailed examination of seasonal behavioral changes, resource selection, and effects of predation by separate assemblages of narwhals in the Baffin Bay ecosystem.

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CHAPTER 1
BACKGROUND AND SYNPOSIS

"It is hardly necessary to say that any person taking up the study of marine mammals, particularly the cetaceans, enters a difficult field of research, since the opportunities for observing the habits of these animals under favorable conditions are but rare and brief. My own experience has proved that observation for months and even years may be required before a single new fact in regard to their habits can be obtained."

--Charles M. Scammon, noted whaling captain/naturalist, 1874

The Arctic environment

Understanding the consequences of changing climate for marine ecosystems and the resources they provide to humans remains one of the biggest challenges in ecology. The Arctic, geographically defined as waters north of approximately 66.5°N, is among the most dynamic and sensitive ecosystems on the planet. This region is characterized by large annual changes in temperature, light, primary production, and possibly the most the defining feature, sea ice formation and recession. In the Arctic, the aerial extent of sea ice changes by a factor of 2. Annual ice forms in early fall and peaks in March. Sea ice recedes in spring with warmer temperatures and increasing light and generally reaches a minimum in September. Consequently, the Arctic is a sensitive indicator of climate change because minor climate deviations are amplified by the cascading effects of sea ice on primary and secondary production and food web structure.

Physical and biological shifts suggest pervasive alterations in the Arctic climate are ongoing (Morison et al. 2000, Parmesan and Yohe 2003, Root et al. 2003). In the past 25 years, the extent of annual sea ice has decreased by 3% per decade, with perennial sea ice decreasing at 9% per decade (Johannessen et al. 1999, Vinnikov et al. 1999, Parkinson et al. 1999, Parkinson and Cavalieri 2002, Comiso 2002). Of the alarming 6% global decline in primary production since the 1980s, nearly 70% has occurred at high latitudes (Gregg et al. 2003). Combined with these trends are reports of changing salinity, warmer air and water temperatures (Morison et al. 2000, Wigley and Raper 2001), shifts in thermohaline circulation (Morison et al. 2000, Mysak

2001), and reorganization of marine zooplankton communities (Beaugrand et al. 2002), all of which leave growing scientific consensus that the Arctic climate is undergoing dramatic change.

While due attention has been given to the overall warming of the Arctic, somewhat less notice has been paid to observations that the patterns of climate change are region-specific and non-uniform. Recent studies in the Canadian high Arctic, Baffin Bay, and coastal West Greenland report findings that are markedly different from the hemispheric trends of sea ice reduction. Since 1970, land and sea surface temperatures in West Greenland have displayed significant cooling trends, also reflected in both oceanographic and biological conditions (Hanna and Cappelen 2003). In addition, Baffin Bay and Davis Strait have displayed strong significant increasing tends in wintertime sea ice concentrations and extent, as high as 7.5% per decade between 1979-1996, with comparable increases detected back to 1953 (Parkinson et al. 1999, Deser et al. 2000, Parkinson 2000a, Parkinson 2000b, Parkinson and Cavalieri 2002, Stern and Heide-Jørgensen 2003). It is also important to note that observations on climate change in the Arctic, and particularly in the West Greenland region, date as far back as the early 20th century where changes in temperatures, biological populations, and sea ice were initially documented (Jensen 1939). The unique regional changes in the Baffin Bay region leave countless questions about the effects of increasing sea ice on the ecosystem structure and the top predators that inhabit the system.

In addition to the direction of climate change, the temporal scale over which change occurs is important because rapid shifts in ice conditions and production will send cascading effects through the food web (Hansen et al. 2002). Abrupt and radical changes have been documented in the North Atlantic region from ice core drilling in Greenland, shifts as extreme as a 7°C increase in temperature over 50 years (Dansgaard et al. 1989, Dansgaard et al. 1993). The potential for rapid change in trophic relationships has challenged marine researchers to integrate high Arctic sea ice dynamics into ecological models, assimilating data from all levels of the food web (Hansen et al. 2002, Hunt et al. 2002, Hunt and Stabeno 2002). In the case of top marine predators, particularly the marine mammals, biological responses to climate have been difficult to ascertain because complex shifts in life history or behavior are often involved. Process-oriented studies identifying the biophysical coupling required to maintain suitable prey availability and ice-associated habitat for marine mammals on regional Arctic scales are critical in light of the changes that may differentially effect sub-populations of a single species (Tynan and DeMaster 1997). Top predators such as Arctic cetaceans, can be monitored remotely and tend to integrate variability in the productivity of the ecosystem across large spatial and temporal scales. These features, together with their position at the top of the food chain, make them ideal candidates for shedding light on ecosystem variability. Arctic cetaceans are considered important indicator species because their seasonal movements, distribution, resource selection, and life history parameters are tightly linked with changes in the Arctic environment, making them both vulnerable to climate alterations and good indicators of cumulative changes (Tynan and DeMaster 1997).

Study species

The narwhal (*Monodon monoceros*) is an Arctic cetacean (Vibe 1967, Mitchell 1984), perhaps the most northerly cetacean in the world. Sharing the category of true "Arctic cetacean" with only the beluga (*Delphinapterus leucas*) and the bowhead whale (*Balaena mysticetus*), narwhals have the most restricted distribution, occupying waters only in the Canadian high Arctic, Baffin Bay, and West and East Greenland (Figure 1.1). The narwhal is an odontocete and a member of the family Monodontidae. It is perhaps best known by the single tooth or tusk, sometimes exceeding 3 m, protruding from the upper left jaw of males. The word narwhal is Scandinavian with "nar" meaning "corpse". Thus, "corpse whale" refers to the mottled black and white skin of the species, which resembles that of a drowned man. Narwhals range up to 4 m in length and may weigh 1,600 kg. Narwhals are important species in subsistence harvests in both Canada and Greenland. In these areas, they are reliably taken for meat, blubber, and tusks following their highly predictable movement patterns and timing.

Seasonality and site fidelity are perhaps the two largest factors contributing to narwhal behavior. Narwhals undergo extensive annual migrations coinciding with extension and residency of sea ice. In the summer months with open water, narwhals visit inshore bays and fjords in the Canadian archipelago and West Greenland. In the autumn, upon the formation of fast ice, narwhals move south over a thousand kilometers and spend the winter in Baffin Bay and Davis Strait, in discrete wintering grounds covered by dense offshore pack ice. Narwhals display extremely high site fidelity to summering and wintering grounds, migration routes, timing of movements, and residency periods on the summering and wintering grounds. This allows for comparative analyses between discrete sub-populations. There appear to be two discrete wintering quarters in central Baffin Bay, one used by narwhals from Creswell Bay, Somerset Island (referred to as the Northern Wintering Ground) and another used by narwhals from in Melville Bay, West Greenland and Tremblay Sound, Baffin Island (referred to as the Southern Wintering Ground) (Heide-Jørgensen *et al.* 2001, Heide-Jørgensen *et al.* 2002a).

Because narwhals are essentially inaccessible to humans for most of the year, most of the information on the species comes from coastal summer observations, harvest records, or remote telemetry. This renders every piece of data on this species highly valuable and requires that both creativity and imagination be used to glean scientific knowledge during the inaccessible offshore periods. Much of the data used in models throughout this dissertation were obtained via hands-on work with live or dead narwhals. For example, satellite telemetry data were obtained from over 30 narwhals live-captured in nets and instrumented with satellite linked time-depth recorders on the dorsal ridge or tusk. Life history data including weight at age, size of sex organs, and length and weight at sexual maturity were collected from harvested narwhals and used as parameters in bioenergetics models. Furthermore, stomach contents were collected from over 90 narwhals harvested in Canada and Greenland between 1994-2002 and used to document seasonal feeding habitats and prey choice. Throughout this dissertation is it clear that such an approach results in many revelations about narwhal movements, foraging behavior, and vulnerability to anthropogenic and climate-induced change.

Objectives

The title of this dissertation should be interpreted broadly, as “space use” is not merely a matter of geography, but is rather closely linked with species’ biology, physiology, ecology, and life history. Patterns of space use, as revealed by movements and behavior in different habitats, can reveal resource choice, habitat selection, and geographic regions that are important for life history and phenology. The two basic objectives for this dissertation were 1) to investigate how the spatial and temporal distributions of resources are manifested as constraints on narwhal movements and habitat selection in the high Arctic, and more broadly, 2) to develop methods for deriving resource selection and habitat use models from satellite-linked radio telemetry data. The following seven chapters quantify spatial and temporal habitat associations of narwhals in high Arctic Canada and Greenland using data derived from satellite telemetry movements, diving behavior, and remotely sensed environmental parameters. Narwhal habitat selection was examined and evaluated relative to population viability in relation to prey resources and natural or anthropogenic changes in the highly specialized pack-ice habitat. The results of this research identify processes key to determining effects of climate change on adaptation, fitness, and survival, and demonstrate that narwhals are important indicators for change in the offshore habitats in the high Arctic – a hostile and inaccessible area about which little is known and where few other species can provide similar insight.

Chapters 2 and 3 examine narwhal diving behavior, which displays a strong seasonality following movements and migration patterns. Narwhals are among the deepest diving cetaceans in the world, rivaling sperm whales (*Physeter macrocephalus*), beaked whales (*Ziphiidae* spp.), and deep-diving pinnipeds like elephant seals (*Mirounga* spp.). Detailing this behavior is of interest for physiology, benthic foraging choice, and energetics. The diving behavior examined on summering and wintering grounds was collected using two different types of telemetry devices. In Chapter 2, Time-Depth Recorders (TDR) were deployed on narwhals during summer. These instruments collected detailed diving parameters, surface time, and dive profiles at resolutions of 1 second or more. TDRs only collect data on the order of days or weeks and must be retrieved from the whale. Therefore they are designed to float after falling off equipped with a VHF transmitter for easy retrieval. In Chapter 3, histogram-structured dive data were obtained from satellite linked time-depth recorders (SLTDRs). These instruments more broadly quantify and summarize diving behavior by binning data into different depth ranges across specific time intervals. Although some resolution is lost with this type of instrument, SLTDRs do not need to be retrieved from the animal and therefore can remotely collect data for many months. Both chapters discuss observed diving behavior in the context of seasonal habitat selection and foraging possibilities. It is currently unknown what the maximum dive limits are for narwhals primarily because of instrument technology and resolution. Narwhals are clearly limited by an aerobic dive limit, however appear to reach depths below 1,500 m regularly during winter. In Chapter 3, dives are enumerated in bins up to a ">1,500 m" depth threshold, yet the maximum depth of the average 12 dives/day to this category remains a mystery. The deep-diving behavior of narwhals is most frequently observed during the winter, when narwhals inhabit waters >2,000 m deep. However, based on TDR deployments in summer where narwhals reached the bottom many times (depths >250 m), it appears narwhals utilize bottom depths in their habitat year-round.

Diving data are often used to draw conclusions about foraging behavior because they enable quantification of trips to different parts of the water column allowing for hypotheses about prey choice. The seasonality of narwhal feeding intensity, predation, prey choice, and impacts on prey species were examined in Chapters 4 and 5. Up until now, information on narwhal feeding behavior has primarily been collected during summer from the stomachs of harvested animals. This is the period when narwhals are most accessible to hunters and most stomachs are examined. This has, however, imposed seasonal constraints on knowledge of year-round feeding habitats because the data are restricted to a few open water months. Chapter 4 presents the first information on stomach contents from narwhals in late fall and winter, data collected at the only accessible fall and winter coastal harvest sites within the narwhal's worldwide range. Results indicate the majority of annual feeding takes place during fall and winter on the lower Arctic wintering grounds. Chapter 4 also supports previous documentation of seasonality in prey choice (Finley and Gibb 1982). Arctic cod (*Arctogadus glacialis*) and polar cod (*Boreogadus saida*) are taken sporadically in summer bays and fjords, yet narwhals switch to Greenland halibut (*Reinhardtius hippoglossoides*) and *Gonatus* squid species in fall and winter (Vibe 1950, Finley and Gibb 1982, Heide-Jørgensen et al. 1994). Chapter 5 brings the foraging seasonality a step further by examining predation on the wintering grounds using bioenergetic and spatial models. Biological parameters collected from harvested animals were used to establish a predation model for sub-populations of narwhals wintering in Baffin Bay. This model produced estimates of removal of Greenland halibut under a series of predation scenarios. This information was related to the spatial distribution of Greenland halibut, collected from 3 years of trawl survey data in Baffin Bay between 1999-2001. Results suggest narwhals clearly impact densities and length frequencies of Greenland halibut in their wintering grounds. This may be due, in part, to the fact narwhals are highly restricted in their movements on the wintering grounds because of extremely dense pack ice. This physical restriction essentially forces whales to share just a few leads and cracks for air, and in combination with the deep and frequent winter dives, results in very focused benthic foraging in a small area on the bottom.

Predation and resource use are tightly linked with habitat choice, and accordingly, Chapters 6, 7, and 8 focus on linking movements and behavior to the dynamic Arctic environment though quantitative spatial modeling techniques. Chapter 6 explores a novel technique for movement analysis: fractal dimensions for comparing and contrasting seasonal movements and population strategies. Fractal dimensions index the linearity of a movement path over replicate temporal scales and can be used to infer the use of landscape from behavior within specific habitat types. Different narwhal sub-populations have different fractal dimensions across seasons, possibly indicating divergent region-specific patterns on the wintering grounds in response to sea ice characteristics. Sea ice dynamics were further explored in Chapter 7, where ice concentrations and the fraction of open water were quantified on wintering grounds between November and March. Using a 22-year time series (1979-2001) of approximate sea ice concentrations from microwave SSMR/SSMI passive brightness temperatures, less than 3% open water was estimated to be available to narwhals on the wintering grounds between 15 January and 15 April, reaching minima of 0.5% open water at the end of March. Significant decreasing trends in the fraction of open water were found in the month of March for the northern wintering ground, with a similar decreasing but non-significant trend found on the southern wintering ground. This decrease in open water is cause for alarm, as the limited number of leads and cracks, in combination with the high site fidelity, makes narwhals exceedingly vulnerable to ice entrapments. A further complication is the remote, offshore location of wintering quarters, together with the low precision in summer abundance estimates, which make it difficult to detect population impacts on sea ice entrapments. In Chapter 8, multivariate habitat models were developed to link concurrently movements, diving behavior, and environmental parameters in efforts to explain seasonal habitat choice and resource use. Models suggest behavior is highly dependent on the environment (depth, slope, distance from the coast) and of the environmental variables examined, bottom temperature was most important (when available dates with bottom temperatures were subset and examined). The bottom temperatures and gradients selected by narwhals during winter correspond well with cool temperatures supporting high densities of Greenland halibut.

It is important to remember that in the dynamic and extreme habitat of the high Arctic, narwhal movements, diving, and resource selection may reflect behavioral traits that have proved successful over centuries or larger time scales, although not necessarily optimal in each year. The marked consistency in annual movement patterns and seasonal habitat selection between sub-populations suggests a learned behavior, probably maternally directed and evolutionarily driven. Although it may be possible to tease out environmental relationships and explain narwhal behavior with measures that we can directly observe and quantify, the survival and persistence of this species in such a harsh and unforgiving environment is, to a certain degree, due to the predisposition for strict patterns and regimented tendencies. Consequently, narwhals may not have the ability to adaptively alter their patterns in light of changing climate, shifts in resource availability, or anthropogenic impacts in the high Arctic.

Figure 1.1. Worldwide distribution of narwhals in the Arctic.

CHAPTER 2

DIVING BEHAVIOR OF NARWHALS AT TWO COASTAL LOCALITIES IN THE CANADIAN ARCTIC

INTRODUCTION

The narwhal (*Monodon monoceros*) is a high Arctic ice-associated cetacean that travels thousands of kilometers each year between shallow, coastal summering grounds and deep, offshore wintering grounds. From July through September, narwhals visit inshore bays and fjords in the Canadian High Arctic archipelago and Greenland. The populations of narwhals that summer in these sheltered waters move south in September to spend the winter months in areas covered by dense offshore pack ice in Baffin Bay and Davis Strait. The diving behavior of narwhals has been studied by both visual observations from coastal promontories on their summering grounds (Silverman 1979, Dueck 1989) and satellite tagging operations (Martin et al. 1994, Heide-Jørgensen and Dietz 1995, Dietz et al. 2001, Heide-Jørgensen et al. 2002a, Heide-Jørgensen et al. 2003a). Narwhals are thought to make relatively shallow dives on their summering grounds, and increase their dive depths in the winter where they feed on Greenland halibut (*Reinhardtius hippoglossoides*), polar cod (*Boreogadus saida*), Arctic cod (*Arctogadus glacialis*), and squid species (*Gonatus* spp.) (Vibe 1950, Finley and Gibb 1982, Heide-Jørgensen et al. 1994). Narwhals are among the deepest diving cetaceans, and have been documented to reach depths of 1,000-1,500 m (Heide-Jørgensen and Dietz 1995, Heide-Jørgensen et al. 2002a, Heide-Jørgensen et al. 2003a).

All of the information on narwhal diving behaviour collected during tagging operations has been from whales instrumented with satellite linked time-depth recorders (SLTDRs) (Martin et al. 1994, Dietz and Heide-Jørgensen 1995, Heide-Jørgensen and Dietz 1995, Heide-Jørgensen et al. 2002a). SLTDRs, the instruments most widely used to study cetacean diving behaviour, collect both an animal’s geographic position and information on dive data. SLTDRs may organize data into a series of depth bins over discrete time intervals or transmit limited amounts of data on diving behaviour just prior to satellite reception. SLTDRs can record large amounts of data and do not need to be recovered from the animal for data retrieval. However, due to constraints imposed by the satellite system (e.g., amount of data, bandwidth, and limited surfacing time of the whales) and battery life, the data collected from these instruments are summarized and compressed, or only fractions of the data are ever transmitted and received by the satellite. This poses limitations on data analysis and interpretation.

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

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

METHODS

Narwhals were live-captured from the beach in Tremblay Sound (72.3°N, 81.1°W) in August 1999 and in Creswell Bay (72.7°N, 94.2°W) in August 2000 (Figure 2.1) using nets set perpendicular from the shore. Tremblay Sound, located on the east side of the Borden Peninsula of Baffin Island, is a long (45 km), narrow (2-7 km wide) fjord. Creswell Bay, located on the east side of Somerset Island (approximately 50 km long and 40 km wide), opens into Prince Regent Inlet. Whales were handled in the nets immediately after they were captured and belts were placed around the mid-section, tail, head, and tusk for restraint. Whales were positioned between two inflatable boats offshore and both SLTDRs and TDRs were attached. SLTDRs (Wildlife Computers, Redmond, WA) were attached to the female whales on the dorsal ridge and to the tusk of males using two stainless steel bands. The dorsal ridge transmitters were attached to the whales with two 8 mm polyethylene pins, secured with nylon washers and nuts. Research was conducted in accordance with principles and guidelines of the Canadian Council on Animal Care. See Dietz et al. (2001) for additional details of SLTDR tag design, attachment, and performance.

The TDRs (Mk7, Wildlife Computers, Redmond, WA) were attached to a flotation device consisting of three oval net buoys held together with 6mm nylon pins, made to withstand pressure at over 400 m. A cylindrical hole drilled in the center of the three buoys contained a VHF transmitter (154 MHz), with an antenna perpendicular to the surface of the water. The TDR was anchored by a lead weight to improve stability. The antenna position provided both successful VHF tracking of the instrumented animal and successful retrieval when the instrument fell off and washed ashore. The TDR and buoys were mounted on the back of the whale behind the blowhole with two suction cups, positioned approximately 10 cm ahead of the buoys and 15 cm apart (Figure 2.2). All tags had a depth range of 0-1,000 m.

The whales were tracked from promontories along the coast with VHF receivers immediately after they were released. Once a constant signal was received, tags were located and retrieved by an inflatable boat. If 24 h had passed and no signal was received, a helicopter search was initiated to retrieve the instrument. When the tags were recovered, the data were downloaded into a PC for analysis. Drift in the depth values was corrected using the software "Zero-Offset Correction v. 1.27" (Wildlife Computers), and data were processed using "Dive Analysis" (Wildlife Computers) to produce summary statistics for each dive. The minimum depth to be considered a dive was set at 8 m for TDR data following previous dive studies for narwhals (Heide-Jørgensen et al. 2001). All dives below this depth were analysed in "Dive Analysis". The TDR sampled pressure (depth), velocity, light level, and temperature every second. From these variables, dive depth, dive duration, ascent and descent rates, and proportional time at depth were calculated.

The SLTDR tags transmitted the number of dives in each of 14 depth and 10 duration bins for each of 4 six-h periods of the day. The proportion of time at the surface, mean dive depth, and mean dive duration were calculated for each complete sampling period from the SLTDR data and from the TDR data during the same temporal periods. Only 6-h periods with both complete SLTDR data sets and complete TDR sampling were compared. Results were compared for three individuals. The TDR data were analyzed with respect to SLTDR programming, where depth to be considered a 'dive' and depth to be considered the 'surface' varied by individual. Mean dive depths for the SLTDR data were calculated using the midpoint of each depth bin using the following formula:

$$meandepth_i = \sum_{j=1}^{14} middepth_j * dives_{ij} / totaldives_i$$

where meandepth$_i$ = average dive depth for period i; middepth$_j$ = middle value of the depth category j; dives$_{ij}$ = number of dives in depth category j for period i, and totaldives$_i$ = total number of dives in period i. Mean dive durations for the SLTDR data were calculated using the following formula:

$$meanduration_i = \sum_{j=1}^{10} midduration_j * dives_{ij} / totaldives_i$$

where meanduration$_i$ = average dive duration for period i; midduration$_j$ = middle value of the duration category j in period i; dives$_{ij}$ = number of dives in duration category j for period i, and totaldives$_i$ = total number of dives in period i. The level of significance was 0.05 for all *t*-tests, regressions, analysis of variance (ANOVA) tests, and post hoc analyses.

RESULTS

Tremblay Sound

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

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

Creswell Bay

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

Dive profile and dive rate

In Tremblay Sound, MM-1 made regular deep dives between 100 and 200 m and stayed at the surface for long periods (Figure 2.3a). The average depth of dives for this individual was 50.8 m (SD = 43.8, *n* = 100) (Table 2.1). The number of dives/h ranged from 1 to 13, with an average of 7.1 dives/h (SD 3.2) below 8 m. In contrast, MM-2 made multiple shallow dives with shorter surfacing periods, and only reached depths below 100 m three times (Figure 2.3b). The average depth of dives for this individual was 23.0 m (SD = 28.4, *n* = 125). Number of dives/h below 8 m ranged from 9 to 13 with an average of 10.9 dives/h (SD 1.2) below 8 m. The deepest recorded sounding in Tremblay Sound is approximately 270 m (National Ocean Service, NOAA, USDOC) and maximum dive depth for both individuals was 256-258 m. Therefore, it appeared the whales were diving to the bottom of their habitat during the period they were tracked.

The dive profiles for the two narwhals tagged in Creswell Bay (MM-3 and MM-4) are similar (Figs. 2.3 c and d). Both whales made multiple short, shallow dives over the course of the tracking period. The average depth of dives for MM-3 was 20.8 m (SD = 14.8, *n* = 36) and the average depth of dives for MM-4 was 34.4 m (SD = 16.1, *n* = 277) (Table 2.1). The number of dives/h for MM-3 ranged from 3 to 9, with an average of 6.0 dives/h (SD 2.2), where as the number of dives/h for MM-4 ranged from 3-14, with an average of 8.3 dives/h (SD 2.6) (Table

2.1). The deepest recorded depth sounding in Creswell Bay is approximately 80 m (National Ocean Service, NOAA, USDOC) and maximum dive depths were 73-75 m, again indicating the whales dove to the bottom of their habitat.

A typical dive profile for all four whales included a steep descent, a short period at the bottom, a slower ascent, and a slow approach to the surface (Figure 2.4). Less typical dives included a stepwise descent, perhaps following the bottom topography, with short periods at the bottom and a steep ascent. Dives with stepwise descent and ascent rates and variation in depth at the bottom were rare. Most dives could be classified as V-shaped, with slightly more bottom time than that reported for a V-shaped dive in Martin et al. (1994).

Dive duration and surfacing time

The mean dive duration for MM-1 and MM-2 was 4.9 min (SD 4.5) and 2.6 min (SD 1.7 min), respectively. The maximum duration of a dive for MM-1 was 26.2 minutes, where as the maximum dive duration for MM-2 was 11.5 minutes (Table 2.1). Using all dives, there was a strong significant relationship between the maximum depth of a dive and the duration of that dive (MM-1: $r = 0.783$, $p < 0.0001$, MM-2: $r = 0.7310$, $p < 0.0001$).

Both whales had similar mean durations of surfacing time (where the surface was defined as depths ≥8 m). The mean surfacing interval for MM-1 and MM-2 was 3.1 min (SD 4.3) and 3.2 min (SD 3.2), respectively (Table 2.1). The most frequent surfacing interval for MM-1 was between 0-1 minutes ($n = 21$) and the most frequent surfacing interval for MM-2 was between 1-2 minutes ($n = 35$). Eighty-two percent of the surfacing intervals were less than 5 minutes in duration for MM-1, and 87% of the surfacing intervals were less than 5 minutes in duration for MM-2. One long surfacing interval for MM-1 (32 min) occurred just after the first deep dive and two of the long surfacing intervals for MM-2 (22 min) occurred right after release (the other occurred approximately 11 h into the tracking period). This second long surfacing interval for MM-2 did not seem to be related to bouts of deep diving, because it occurred in the middle of a series of shallow (13-25 m) dives. Post-dive surface time was significantly correlated with depth of dive for MM-1 ($r = 0.295$, $0.002 < p < 0.0005$), however, surface time was not significantly correlated with depth of dive for MM-2 ($r = 0.14177$, $0.1 < p < 0.2$). Post-dive surfacing time was significantly correlated with dive duration for both MM-1 ($r = 0.233$, $p = 0.02$) and MM-2 ($r = 0.213$, $0.02 < p < 0.05$).

The mean dive duration for MM-3 and MM-4 was 3.4 min (SD 1.6) and 4.3 min (SD 1.7), respectively. The maximum dive duration for MM-3 was 7.0 minutes and the maximum dive duration for MM-4 was 9.4 minutes (Table 2.1). Using all dives, there was a strong relationship between the maximum depth of a dive and the duration of that dive (MM-3: $r = 0.741$, $p < 0.0001$, MM-4: $r = 0.815$, $p < 0.0001$).

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

Ascent and descent rate

Velocity data from MM-1, MM-2, and MM-3 were high for the first dive after the tag was deployed. However, this same velocity was observed later during normal behaviour for all three whales. Mean descent rate was strongly correlated with destination depth for MM-2 and MM-4 (MM-2: $r = 0.666$, $p < 0.001$, MM-4: $r = 0.275$, $p < 0.001$), slightly correlated with destination depth for MM-3 ($r = 0.372$, $0.02 < p < 0.05$), and was not correlated with destination depth for MM-1 ($r = 0.094$, $p > 0.2$). There were no statistically significant relationships found between mean ascent rate and mean descent rate for each whale (reported in Table 2.1). There was a significant difference between ascent rates (ANOVA, $p < 0.001$) and descent rates (ANOVA, $p < 0.001$) between individuals. A Tukey-Kramer post hoc analysis revealed the significant differences occurred on both ascent and descent rates between MM-1 and the other three whales.

Proportion of time at different depths

Only the two tags from Tremblay Sound provided the resolution necessary for calculating the percentage of time spent within specific depth bins (Table 2.2). MM-1 and MM-2 spent approximately 49.3% and 70.5% of the time, respectively, within 10 m of the surface. It is clear that MM-1 spent more time at deeper depths (between 20-100 m) than MM-2. Figure 2.5 a and b (binned into intervals to match Martin et al. (1994)) visually demonstrate that the whales were using the water column differently. MM-1 spent approximately one-fifth the amount of time in the 0-1 m category and approximately one-third the time in the 1-3 m category as MM-2.

TDR and SLTDR comparison

Dive data from TDRs and SLTDRs deployed simultaneously were compared for three individuals (MM-1, 2 and 4) in this study. Because attachments times for the TDRs varied, only small amounts of data could be statistically compared. Although TDR attachment overlapped with 13 6-h periods for the three whales, we report only results from full 6-h periods with complete TDR and SLTDR records, obtained as follows: one period for MM-1, one period for MM-2, and 5 periods for MM-4 (Table 2.3). For this comparison due to SLTDR set-up, a dive was defined as > 8m for MM-1 and MM-4, and > 12 m for MM-2.

Surface time was approximately 11% higher for the SLTDR than the TDR for MM-1, 5% higher for MM-2, and varied for MM-4, where the first two temporal periods were 2-3% higher for the SLTDR, and last three temporal periods were approximately 1% lower (Table 2.3). Mean dive depth and mean dive duration of the SLTDR were lower (in all but one period) than the TDR data. When the five temporal periods were combined for MM-4 (the only individual where the TDR remained on for longer than a single 6-h period), there was no significant difference in mean depth and mean duration from the SLTDR and TDR data across periods (p = 0.75 for depth, p = 0.44 for duration).

DISCUSSION

The recovery of the tags in Tremblay Sound was primarily due to the high cliffs in the area, which were used for long-range VHF signal detection. The recovery of the tags in Creswell Bay was primarily due to helicopter support, where VHF signal direction and strength could be located from an altitude of approximately 2,500 feet. We observed no adverse reaction to the tagging procedure after release, such as prolonged periods at the surface that were not also observed hours into the tracking period or excessively slow movements in the water column. Dive depths and velocity were initially high once the whales were released, however, similar depths and speeds were observed hours into the data collection.

The whales instrumented with TDRs in both Tremblay Sound and Creswell Bay were physically restricted in diving beyond the maximum depths recorded here due to the relatively shallow habitat of their summering grounds. Studies have demonstrated that narwhals are capable of diving to depths over 1,500 m (Heide-Jørgensen et al. 2002a). Most of these records come from the whales wintering grounds in Baffin Bay and Davis Strait, where water depths reach over 2,500 m. The data presented in this study are probably representative of typical narwhal behavior on their summering grounds, as other studies have reported similar dive statistics during the same season (Heide-Jørgensen and Dietz 1995, Heide-Jørgensen et al. 2001). It appears that narwhals use the deepest parts of the water column in both summering and wintering areas.

The two whales tagged in Tremblay Sound exhibited clear differences in diving behavior, which could not be attributed to sex or body size, as both whales were males in the same size class. In Tremblay Sound, MM-1 made longer, deeper dives and spent less time at the surface than MM-2 (Figs. 3 a, b, and 5). The differences between the whales could be related to individual differences in foraging and diving capabilities, or site-specific behavior. Only MM-1 had a significant correlation between post dive surfacing duration and depth of dive, which has been interpreted as reaching an aerobic limit (Boyd 1997, Kooyman and Ponganis 1998). However, the correlation between post dive surfacing duration and depth here may not indicate aerobic limitations because much longer dives and deeper dive depths have been recorded for narwhals (Heide-Jørgensen and Dietz 1995, Heide-Jørgensen et al. 2002a, Chapter 3). There have been few studies on the aerobic limits of narwhals. Williams et al. (1987) calculated an aerobic dive limit (ADL) (the maximum dive duration that can be supported by aerobic metabolic processes) for a 1,200 kg narwhals to be 14 min (at a swim speed of 1.5 m/s), or 21 min (at a swim speed of 1.0 m/s). Schreer and Kovacs (1997) also predicted maximum dive depth (1000 m) and maximum dive duration (20 min) for narwhals based on allometric equations related to body mass (estimated as 1,600 kg). Aerobic dive limits have also been examined for the beluga, *Delphinapterus leucas*, (a close relative to the narwhal) and are similar. Schreer and Kovacs (1997) reported an ADL for a beluga of 25 min and Shaffer et al. (1997) reported maximum dive durations of captive belugas of 13.3 min and an empirically determined ADL of 9-10 min.

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

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

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

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

The consistency in dive profiles with little bottom time indicates whales were not actively chasing prey underwater. Statistical classifications of dive shapes and classifications have been published for several species (Schreer and Testa 1995, Lesage et al. 1999, Malcolm and Duffus 2000). We observed only a few dives where direction and shape changed in the water column. Most dives appeared to be V-shaped (Martin et al. 1994, Figure 2.4) with minimal bottom time.

It is possible whales were merely traveling in and between bays and fjords in these regions, or if active foraging occurred, it was not when the whales were being monitored.

MM-1 and MM-2 spent 30.3% and 52.9% of their time in depths < 5 m, respectively (Figure 2.5). These data are fairly consistent with other studies. For example, Heide-Jørgensen and Dietz (1995) reported 40% of the time spent by seven narwhals tagged in Melville Bay, West Greenland was at depths < 5 m (ranging from 35%-64%). In addition, Heide-Jørgensen et al. (2001) reported mean surface time above 5 m as 46.7% and mean time spent above 6 m as 64.0% for narwhals tagged in Tremblay Sound. Martin et al. (1994) reported the time spent above 5 m in depth for one whale tagged in Tremblay Sound as 55.7%.

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

Martin et al. (1994) also reported the proportion of time an adult narwhal spent at different depth bins in Tremblay Sound. Our data (Figures 2.5a, b), when binned into the same categories, gave different results. These differences are not due to location or time of year because data were collected for both studies in Tremblay Sound in the month of August. However, it is possible the difference could be attributed to sex-specific behavior, where Martin et al. (1994) reported their data for a female whale. The tag used in Martin et al. (1994) sensed depth every 40 seconds, and remained on the whale for 15.9 days. To account for differences in sampling rate (where tags in this study sampled depth every 1 s), we re-sampled our data into 40 s increments and arrived with very similar proportions as the 1 s sampling rate.

Studies on pinnipeds comparing TDRs and SLTDRs generally report larger sample sizes (complete sampling periods with both instruments) because instruments can be glued to the fur of the animal and retrieved easily. Our sample size used for the comparison here (7 full 6-h SLTDR periods) represents 42 h of suction cup attachment on the whales, a relatively substantial sample size relative to other cetacean TDR studies (Hooker and Baird 1998, Baird et al. 2001). Recently, there have been several published studies where suction cup attached TDRs have been successfully deployed and retrieved on cetaceans (Hanson and Baird 1999, Hooker and Baird 1999, Malcolm and Duffus 2000, Hooker and Baird 2001, Baird et al. 2001). These studies, however, did not simultaneously deploy, collect, and compare SLTDR data on the same individual.

Our small sample size showed that the estimated proportion of time at the surface (between 0 m and a selected depth) is similar for both TDR and SLTDR data (Table 2.3). These results are similar to that of Burns and Castellini (1998), who, despite a small sample size and a coarser sampling rate than that reported here, found that the two methods were generally comparable. Corroborating SLTDR surfacing data is very important for cetacean abundance estimates. Species-specific correction factors for cetaceans are generally obtained from SLTDR deployments or VHF surfacing signals. TDR data collected for cetaceans are particularly useful for developing correction factors because the high sampling rate (1s) enables a detailed calculation of time at depth between each meter of the water column, where as the SLTDR data are measured every $\geq$10 s and summarized in crude categories. The high-resolution TDR data facilitate the use of a probability estimation technique where the availability at variable depths can be quantified.

Both the mean dive depth and mean dive duration estimated from the TDR were higher (or equal in one case) than that estimated for all complete sampling periods from the SLTDR. There are two explanations for the lower values obtained from the means from the SLTDR. The SLTDR has a 10 s sampling rate, therefore the coarser sampling scheme may underestimate the depths and durations. In addition, the midpoint of a bin (a common technique to obtain mean values from SLTDR data) most likely underestimates the mean depths and durations. Overall, our findings suggest that the dive data collected from the TDRs and SLTDRs are generally comparable. These findings come from a relatively small sample size, where the length of time that the TDR was attached was short relative to the sample sizes necessary for a robust analysis. Future work should target longer sampling periods for cetaceans where results from these two types of tags can be compared.

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

Table 2.1. Summary of dive statistics for narwhals tagged with Time Depth Recorders in Tremblay Sound and Creswell Bay in 1999 and 2000. Mean and standard deviation (SD) are reported for each category (SD in parentheses). DPH is dives per hour or dive rate, D is dive duration in minutes, MD is maximum dive duration in minutes, SI is surfacing interval in minutes, DR is descent rate in m/s, and AR is ascent rate in m/s.

ID	Sex	Body/ Tusk length (cm)	Dive depth (m)	Max depth (m)	Total # dives <8 m	DPH	D	MD	SI	DR	AR
MM1	M	410/118	50.8 (43.8)	256	100	7.1 (3.2)	4.9 (4.5)	26.2	3.1 (4.3)	1.3 (0.8)	1.5 (1.6)
MM2	M	444/178	23.0 (28.4)	258	125	10.9 (1.2)	2.6 (1.7)	11.5	3.2 (3.2)	0.8 (0.4)	0.7 (0.4)
MM3	F	390	20.8 (14.8)	73	36	6.0 (2.2)	3.4 (1.6)	7.0	6.9 (6.6)	0.6 (0.4)	0.6 (0.4)
MM4	F	370	34.4 (16.1)	75	277	8.3 (2.6)	4.3 (1.7)	9.4	2.9 (3.3)	0.6 (0.3)	0.8 (0.3)

Table 2.2. Proportion of time spent at depth for narwhals in Tremblay Sound, reported at a finer scale near the surface (1 m increments between 1-10 m). These data are useful for determining correction factors for availability bias in aerial surveys based on the proportion of time whales are at (or below) a specific depth.

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

Table 2.3. Comparison of dive statistics obtained for narwhals equipped with TDRs and SLTDRs simultaneously. n=number of complete six h periods where both tags were on the whale. Dive summaries for individual periods are listed separately in columns. Surfacing time was set as < 6m for MM-1, and <7m for MM-2 and MM-4. The depth to be considered a dive was > 8m for MM-1 and MM-4, and > 12 m for MM-2.

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

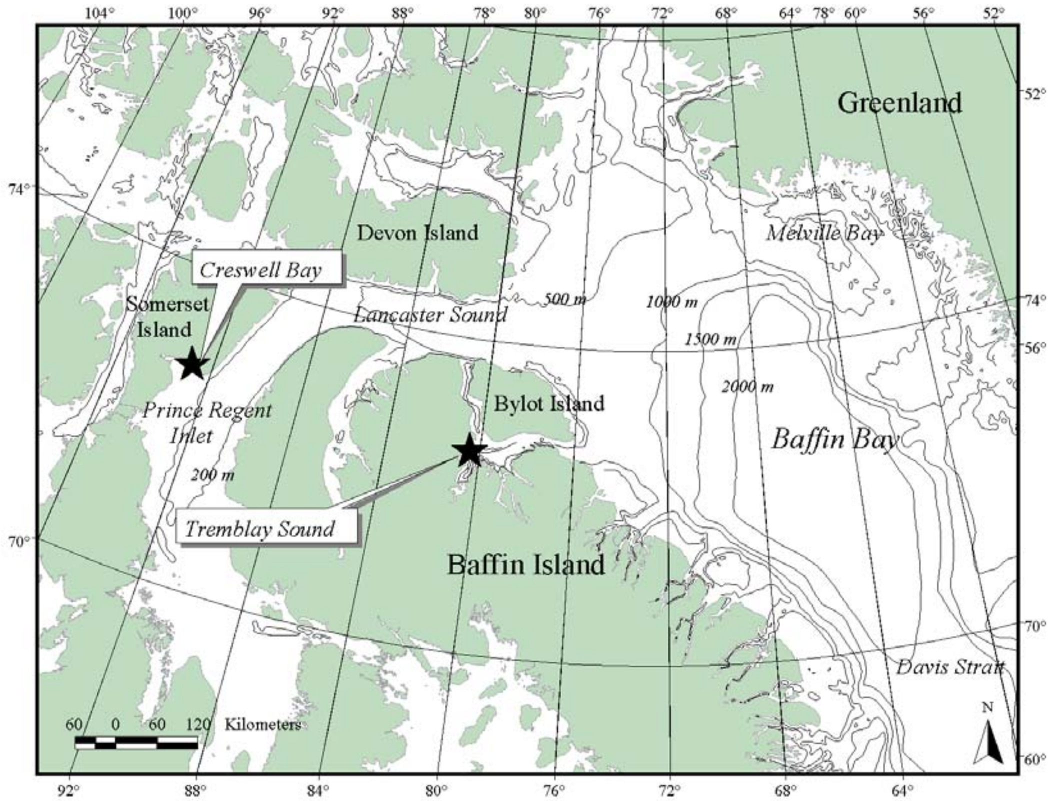


Figure 2.1. Location of Time Depth Recorder tagging sites and place names mentioned in the text. Bathymetric contours are noted on the map.

Figure 2.2. Image of suction-cup attached TDR on a narwhal in Creswell Bay, August 2000. Note the round buoys attached to the suction cup with wire. The TDR is attached underneath the buoy cluster and rests on the whale’s back.

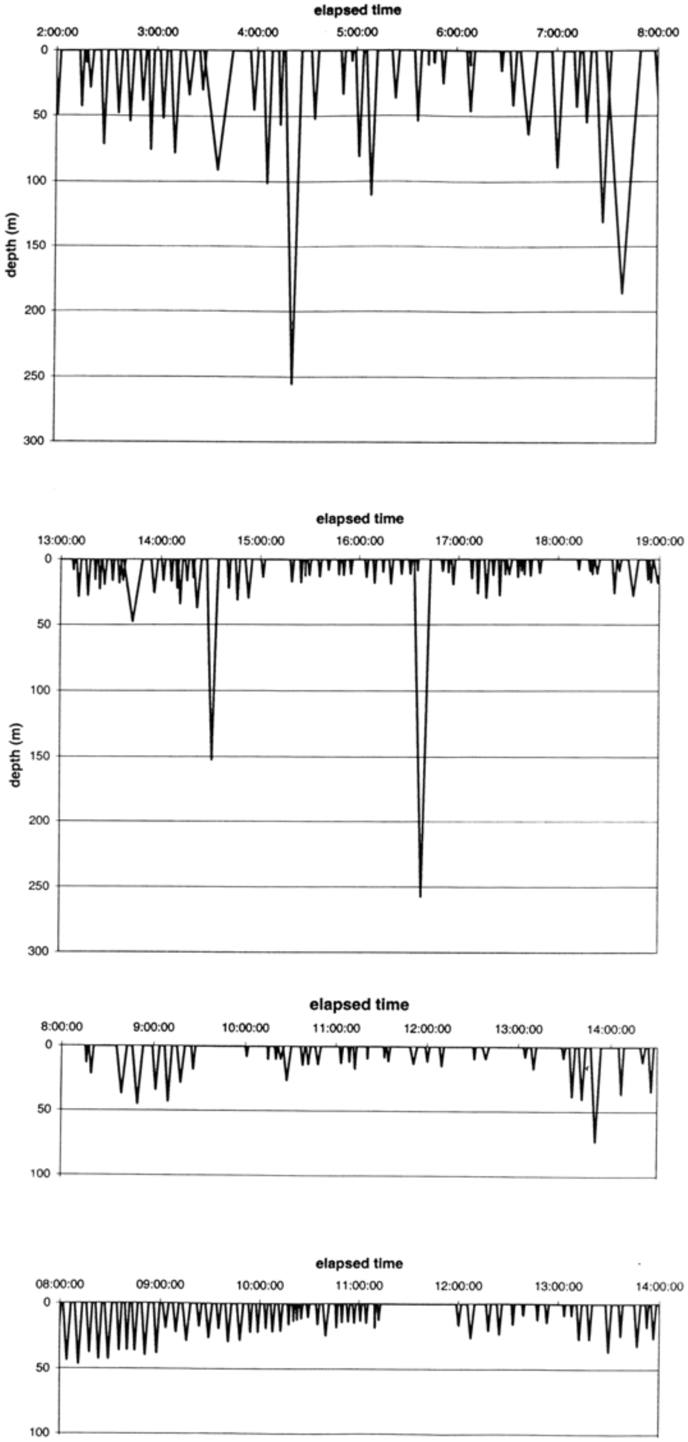


Figure 2.3. a-d. Dive profiles for MM-1 (a), MM-2 (b), MM-3 (c), and MM-4 (d). Only a 6 h portion of the dive profile from each individual is shown here.

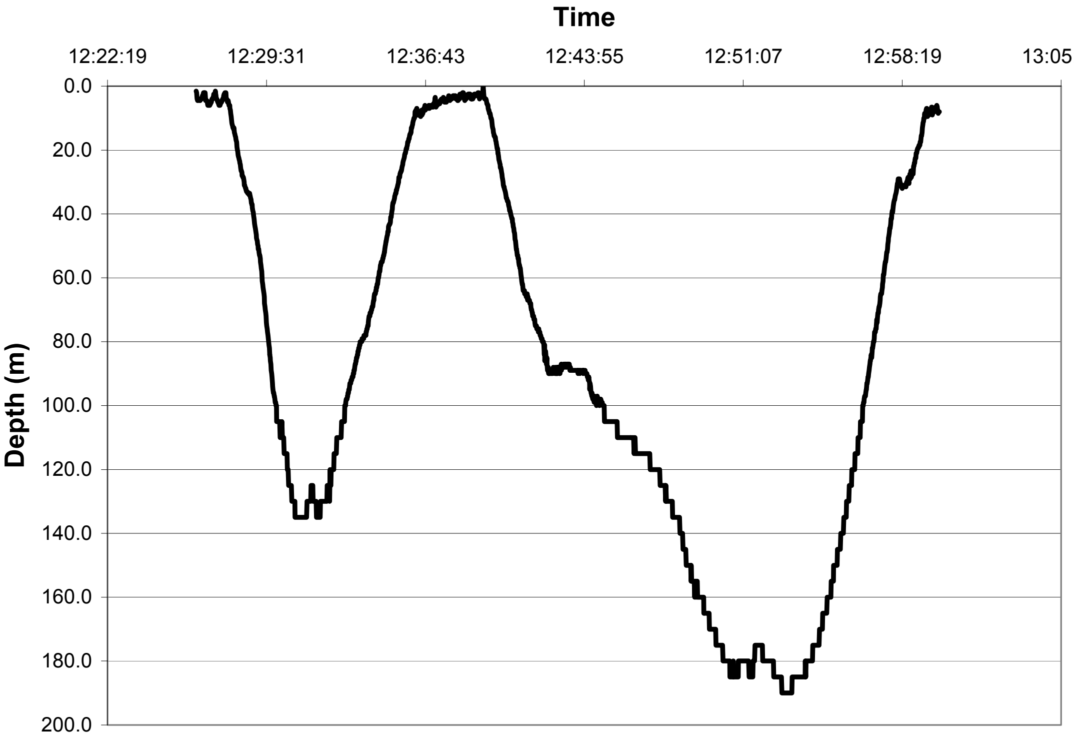


Figure 2.4. Representative dive profile, taken from MM-1. Note the V-shaped dive and limited bottom time.

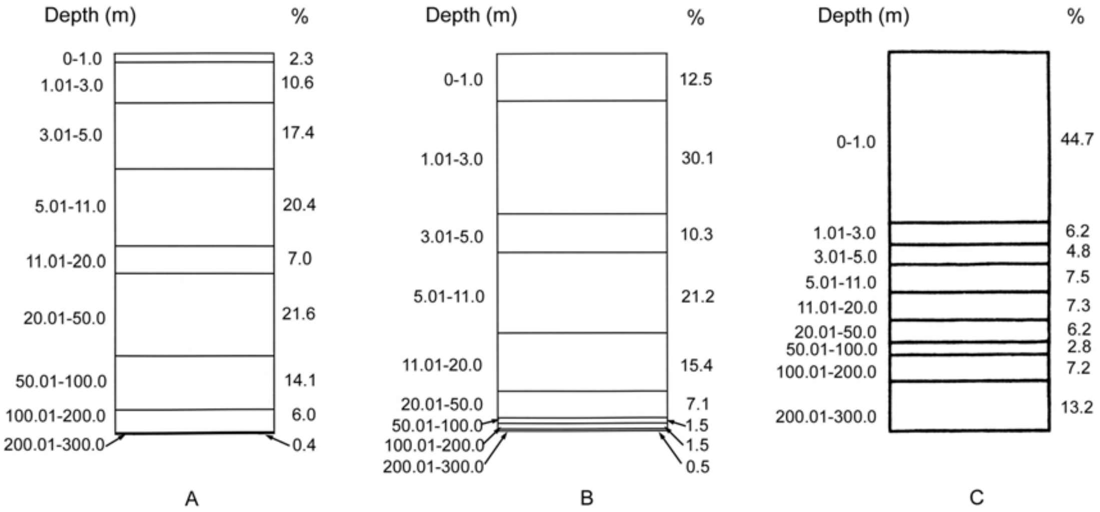


Figure 2.5. Percentage of time at depth from TDR data for (A) MM-1, (B) MM-2, and (C) adapted from Martin *et al.* (1994). Only MM-1 and MM-2 provided detailed enough data to make these comparisons. Data from this study were binned into the same surfacing bins used Martin et al. (1994) to facilitate comparison.

CHAPTER 3
DEEP-DIVING BY NARWHALS: DIFFERENCES BETWEEN WINTERING AREAS?

INTRODUCTION

The narwhal (*Monodon monoceros*) is a year-round inhabitant of Arctic waters bordering the Atlantic Ocean. During July and August, narwhals are widely distributed in large expanses of open water fjord complexes and bays in the eastern Canadian High Arctic and Northwest Greenland. Narwhals make annual long distance migrations between high Arctic summering grounds and wintering grounds farther south in deep, ice-covered waters in central Baffin and Davis Strait, which are occupied between November and April (Dietz and Heide-Jørgensen 1995, Dietz et al. 2001, Heide-Jørgensen et al. 2002a, Heide-Jørgensen et al. 2003a).

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

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

Seasonal differences in dive behavior between sub-populations of narwhals have not been quantified, and it is not clear how behavior may be influenced by summering ground origin or wintering ground location. Information on habitat use during the winter period and divergent behavioral characteristics between sub-populations is critical both due to the potential development of an offshore, deep water fishery for Greenland halibut (*Reinhardtius hippoglossoides*) on the wintering grounds and also in the context of increasing sea ice on the wintering grounds due to climate change (Parkinson et al. 1999, Deser et al. 2000, Stern and Heide-Jørgensen 2003). Sub-population discreteness, together with high site fidelity to wintering grounds, provides the opportunity to examine and contrast the ecology of narwhal foraging in different areas.

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

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

METHODS

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

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

Data were collected from narwhals around Baffin Island and Somerset Island, Canada between 1997 and 2001, and were combined with relevant records from previous published studies conducted in West Greenland in 1993 and 1994 (Dietz and Heide-Jørgensen 1995, Heide-Jørgensen and Dietz 1995). Sixteen narwhals were used in the analysis (6 M and 10 F) where tag attachment lasted well into the late migration or winter period (defined here as beyond November 1, based on Heide-Jørgensen et al. 2002). Thirteen whales were equipped with tags with pressure sensors and three whales were equipped with tags with temperature sensors. Data for each whale were divided into three seasons: summer (tagging date to 15 September), autumn migration (16 September – 31 October), and winter (November 1-end of tag transmissions) and whales were assigned to one of the two wintering grounds based on their destination (Figure 3.1). All tags were deployed between 16 August and 2 September. Pressure transducers sampled the depth of the whale at 4 m (0-1,000 m range) or 6 m (0-1,500 m range) resolution depending on the tag model and year of deployment. SPOT2 tags collected binned 'time at temperature' histograms by sampling temperature every 10 seconds and accumulating proportion of time an animal spent within several water temperature categories (or "bins") between –2 and +3°C. Data on the number of dives in different maximum depth categories and the proportion of time spent in the depth categories were collected in four 6-h periods across each day and summarized into histograms with up to 14 depth categories. Only 6 h periods with available information on the number of dives and the time at depth were used in the analysis. Intervals between surfacings were not considered dives unless a depth of >8 m was recorded (with the exception of two individuals where dives started as 12 m) (Table 3.1). Time spent within a depth category with a duration of <10 s may have been missed because depth data were sampled at that temporal resolution. Dive data were transmitted in segments when the whale surfaced, and were re-assembled using Wildlife Computers software packages (SATPAK). Time spent in different temperature categories by three whales during winter 2001 was related to water depth using CTD casts taken in October 2001 on the northern wintering ground (Jørgensen 2002).

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

Data from 12 male and female narwhals tagged in Eclipse Sound, Canada, between 1997 and 1999 were analyzed to identify potential sex-based biases in dive behavior, particularly deep diving ability. Because the tags with longer duration were not equally distributed across the two sexes, a larger sample size (including tags with shorter duration) was used to examine the number of dives to different depths and time spent at different depths for males and females (ANCOVAs with date as a covariate).

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

$$S_j = \frac{N * D * 2}{TAD}$$

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

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

$$TransitTime_j = 2 * \sum_{i=j+1}^{k} \overline{D}_i * \frac{DepthCatDist_j}{\overline{S}_i}$$

where $\overline{D}_i$ is the average number of dives per day to the ith depth category, k is the index of the deepest depth category, $DepthCatDist_j$ is the vertical length (in m) between the upper and lower limits of the jth depth category, and $\overline{S}_i$ is the average vertical speed from the surface (in m s^{-1}) to the ith depth category.

$RTTimedive_j$ was defined as the time (min) between departure from the surface (where a dive was defined by the tag set up) to the target depth and back to the surface, or:

$$RTTimedive_j = \left[(DiveDist_j / \overline{S}_j) / 60\right] * 2$$

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

Occupancy time (OT_j), the average number of minutes spent in each category per day excluding time spent transiting through the category, was estimated for each individual, or:

$$OT_j = \frac{TotalTime_j - TransitTime_j}{60}$$

where $TotalTime_j$ was the total number of minutes spent in each category per day. The average number of minutes spent in the depth bin on each dive ($OTdive_j$) was simply occupancy time divided by the mean number of dives per day to that depth bin, or:

$$OTdive_j = \frac{OT_j}{\overline{D}_j}$$

The total time (min) for a dive to category_j ($TotalTimedive_j$), including transit time up and down from the surface and time spent in category_j, was then:

$$TotalTimedive_j = OTdive_j + RTTimedive_j$$

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

RESULTS

The 13 dive data tags had a mean attachment time of 106 days (SD 43). The 3 SPOT2 tags had a mean attachment of 124 days (SD 27). The mean number of complete 6-hour periods obtained from the whales during summer, migration, and winter was 86 (range 27-128), 139 (range 61-184), and 114 (range 15-397), respectively (Table 3.1). The selection of a single threshold date to identify the end of the summer period (September 15) was based on the later departure of whales from the summering ground in Melville Bay, and encompassed the typical summer behavior of whales for all three sites.

Locations relative to bottom depth

Daily good-quality ARGOS locations for the sixteen whales (n=1,498 positions) were used to examine differences in depth selection between individuals by sex and season (Table 3.2). A grand mean of maximum bottom depth including all positions across all seasons was 731 m (SD 629, range 2-2,370 m), and means for each season were 265 m (SD 209) for summer, 699 m (SD 601) for migration, and 1,362 m (SD 476) for winter. There was a significant difference between depths used by whales in the northern and southern wintering grounds ($p < 0.001$). Whales in the northern wintering ground were located in deeper water (1,538 m, SD 637, range 380-2,355 m) than those in the southern wintering ground (1,252 m, SD 291, range 303-1,769 m).

Number of dives to depth

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

Parameter estimates of the average number of dives per day to different depth categories displayed clear seasonal patterns, which in some seasons appeared to be divergent for sub-populations (Table 3.3). Near surface dives between 0 and 50 m made up the largest proportion of dives and these excursions are assumed to represent a variety of typical cetacean behaviors such as travel, resting, or milling besides near surface foraging. The average number of these dives declined between summer and winter for the three sub-populations (reduced by approximately 50%) (Table 3.3). These near surface dives were excluded from analyses when examining dives to deeper depths. Although the number of dives to different depths varied in summer and during migration for the three sub-populations, the overall patterns were similar with the most pronounced seasonal differences detected during the winter period. Narwhals from Somerset Island (390-402 cm length) made many more dives to mid-water depths than narwhals from both Eclipse Sound (410-475 cm) and Melville Bay (>400 cm), yet deeper dives were the apparent preference for the sub-populations from Melville Bay and Eclipse Sound (Figure 3.2a-c). A selection of mid-water depths farther north was clearly in contrast to selection of deep depths farther south.

In winter, three male narwhals from Eclipse Sound dove approximately 13 times per day to depths >800 m (SE 1) yet made only 5 dives (SE 3) to the mid-water depth category of 200-400 m (Figure 3.2a). Narwhals from Melville Bay made 26 dives day^{-1} to >800 m (SE 3), yet this sub-population only made 3 dives day^{-1} (SE 6) to 200-400 m (Figure 3.2b). In contrast, Somerset Island narwhals made 25 dives day^{-1} (SE 3) to the 200-400 m depth category. The number of dives day^{-1} to deeper depths (>800 m) for this sub-population was 5 dives (day)$^{-1}$ (SE 1) (Figure 3.2c). The 95% confidence interval (CI) encompassing the parameter estimates for deep dives for both Eclipse Sound and Melville Bay did not overlap with the 95% CI for Somerset Island for this depth category. One of the whales from Eclipse Sound was equipped with a tag capable of recording very deep dives (>1,400 m). When the 13 dives day^{-1} >800 m for this whale were examined at this resolution, almost 50% of the dives exceeded 1,400 m (6 dives, SD 0.5). Furthermore, 5 dives day^{-1} reached 1,200-1,400 m (SD 0.4), 1 dive day^{-1} between 1,000 and 1,200 and 1 dive day^{-1} between 800-1,000 m. Upon examination of models for pooled whales on the two wintering grounds, a clear focus on dives to >800 m was found on the southern wintering ground (16 dives day^{-1}, SE 1.5), whereas fewer deep dives (5 dives day^{-1}, SE 1.6) and five times as many mid-water dives (25 dives day^{-1}, SE 3) were estimated to occur on the northern wintering ground.

The sex-specific dive behavior comparison including tags with shorter longevity during the summer and autumn migration period (13 August to 1 November) was based on 2,106 6-hour periods, examined for differences in the number of dives to different depth categories for males (n = 4) and females (n = 8). When dives to depths of 400 m and greater were examined at 100 m increments, significant differences between sexes were found in the 500-600 m depth category (p = 0.01), 700-800 m depth category (p = 0.004) and >900 m (p < 0.001) depth category (ANCOVA). In all cases, females performed significantly more dives per day to these depths than males. When the number of dives to deeper depth bins were pooled and males and females compared, both for dives >600 m and dives >700 m, females made more deep dives per day than males (ANCOVA, p < 0.001 for >600 m, p < 0.001 for >700 m). In general, these results suggest no differences in diving performance between males and females, except that females make more dives to deeper depths than their male counterparts.

Absolute proportion of time at depth

Model estimates of the absolute proportion of time spent in each depth category (in hours) by season followed similar patterns as those observed with number of dives (Table 3.3) where time spent between 0-50 m declined from summer to winter. The parameter estimates of absolute time at depth per day by wintering ground (Figure 3.3) demonstrated striking differences between the allocations of time in the water column. In the northern wintering ground, the largest proportion of time was spent between 200-400 m (over 3.6 hours, SE 0.5), with a steep decline towards deeper depths, where on average, whales spent slightly over 0.7 hours (SE 0.1) >800 m. In contrast, on the southern wintering ground, whales spent over 3 h per day (SD 0.1) at depths >800 m (6 times more than the northern wintering ground), and between 1.4 h (SE 0.6) to 2.6 h (SE 1.2) hours per day at depths between 100-400 m, which include the time spent traveling through these depths to reach the >800 m destination depths (Figure 3.3). Data collected from the high-resolution tag from Eclipse Sound indicated that of the daily average of 3 hours >800 m in the winter, 30 minutes were spent at depths >1,400 m, 45 minutes spent between 1,200-1,400 m, 48 minutes between 1,000-1,200, and 52 minutes between 800-1,000 m.

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

Proportion of time in temperature ranges

Three female narwhals collected time at temperature data on the northern wintering ground in 2001. After November 1, the proportion of time spent in specific temperature categories was concentrated in two ranges: 34% of the time was spent between –1.2 to –1.6 ^{o}C (SD 15) and 25% of the time was spent between 0.3 to 1.7 ^{o}C (SD 11) (Figure 3.4). The lowest proportion of time (2%) was in the warmest temperature category, between 2.3 to 2.8^{o}C. Two CTD casts, taken on the northern wintering ground in 2001 (Figure 3.5), showed that the warm temperature category (2.3-2.8^{o}C) occurred in two depth ranges: 0 to 20 m (Figure 3.5 inset) and 300-600 m. In November and December 2000, whales in the northern wintering ground spent on average 34% (SD 8) of their time at depths <8 m (based on 165 6-hour periods of surfacing data after November 1). Given this surfacing time estimate, even if the surface water cooled between the CTD measurements in the month of October and the whales arrival in the month of November, the proportion of time spent in the three warmest depth categories (31%) does not allow for much diving behavior below 350 m, as whales must pass through this warm water thermocline layer to reach depths greater than 600 m, corroborating dive behavior recorded in 2002 using direct depth measurements.

Dive profiles and Occupancy Time

Vertical speeds were calculated from 1,587 dives with a terminal destination depth from narwhals tagged between 1993-2000. The magnitude of the speed was significantly related to the destination depth and the vertical distance of the interval over which the speed was calculated (Figure 3.6). Note, there were no female narwhals with 1,500 m resolution tags, therefore, no estimates of speeds beyond 850 m are available for this sex. An average vertical speed was used in the time budget model between 0 and 50 m (0.41-0.45 m s^{-1}) and to depths of 800 m and greater (1.86 m s^{-1}) (Figure 3.6).

Average daily occupancy time in each depth category (AOT_j) varied significantly between wintering grounds (Table 3.4). Whales in the northern wintering ground spent, on average, over 2.6 h day^{-1} (SD 0.4) occupying the 200-400 m depth category, while whales on the southern wintering ground spent, on average, only 0.6 h day^{-1} at this depth (SD 0.4). In contrast, whales in the southern wintering ground spent on average over 3 h day^{-1} (SD 0.6) occupying depths >800 m, where as whales from the northern area only spent 0.7 hrs (SD 1) at this depth. Note, if maximum dive depths were actually deeper than 800 m, some proportion of occupancy time calculated here would actually be composed of transit time. For mid-water depths (100-400 m) average occupancy time per dive ($AOTdive_j$) was not different between the two wintering grounds (Table 3.4). For dives to depths >800 m, $AOTdive_j$ was twice as long in the southern wintering ground, indicating whales in this area spend more time on each dive occupying deep depths. Round trip transit time was positively correlated with depth and was the same for both wintering grounds. Specifically for the bins of interest to this study, round trip transit time was 5 min (SD 0.3) per dive to 200 m, 8 min (0.2) per dive to 400 m, and approximately 13 min (SD 0.5) per dive to >800 m.

DISCUSSION

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

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

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

The observations on the number of dives to mid and deep-water depth categories and the proportion of time spent in those categories may indicate site or sub-population specific selective use of the water column. There are several possible explanations for the divergence in behavior, including differences in habitat structure, prey availability, or innate adaptations between sub-populations. Whales in the northern wintering ground are spread between the continental shelf and the Baffin Bay abyss (Figure 3.1). These narwhals occupy deeper water (significantly deeper than those farther south). The southern wintering ground is more elongated, located precisely along the 1,400 m depth contour with a maximum depth recorded for whale locations of 1,750 m. Based on the similarity in behavior for multiple narwhals in the area (many dives day^{-1} exceeding 800 m) and the narwhal with the high-resolution tag (50% of dives >800 m exceeded >1,400 m), it appears that narwhals rely heavily on foraging on the bottom in this region. Curiously, whales in the northern wintering ground have access to deeper depths yet make shallower dives. It is possible that whales in this area spend more time in mid-water not because they directly select for shallow depths, but because reaching the bottom is more costly or impossible. Alternatively, if narwhals specifically target mid-water depths, the maximum bottom depth in their range may not be an important factor in their choice of location. The maximum limit of the pressure transducer prevented recording the deepest dive depth therefore actual maximum depth was unknown.

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

It is likely that not all dives are directed towards specific depths, and foraging time may quite possibly include searching at multiple depths for prey patches. Histogram-structured data potentially mask this and may suggest individuals are not selective in their utilization of the water column if they dive to the bottom in habitats with different bathymetric structure. Parameter estimates describing the number of dives per day or absolute time per day in a depth category are not independent from estimates for other depth categories. In particular, the estimates for each depth category were derived using independent depth-specific models, however the estimates are not independent from each other. In the case of binned data, the depth category where the number of deep dives peaks is an indication of dive focus, yet the absolute value will vary in different habitats. The modal number of dives on the southern wintering ground (bottom dives) is less than (almost half) that for mid-water dives on the northern wintering ground. This disparity likely arises due to temporal and physiological constraints on diving to deep vs. mid-water depths. Thus, it is likely that the whales decide to make a deep dive at or close to the surface. This hypothesis is also supported by the asymptotic behavior of vertical speeds as depths approach 500 m (Figure 3.6).

The vertical distribution of narwhal prey in the water column influences feeding behavior and dive tactics. In summer narwhals feed on Arctic cod (*Arctogadus glacialis*) and Polar cod (*Boreogadus saida*) at the ice edge, shifting to deep-water prey species such as Greenland halibut or *Gonatus* squid in early fall and winter (Finley and Gibb 1982). Directed foraging on high densities of Greenland halibut requires that narwhals dive to at least 800 m, as surveys for Greenland halibut in the wintering grounds report highest densities between 800-1,200 m (Treble et al. 2000, Treble et al. 2001, Jørgensen 2002). Based on our model, diving to these depths requires a travel time of 14-15 min per dive, allowing no more than 11 min of foraging time per dive for a maximum submergence of 25-26 min based on estimates of aerobic dive limits (Schreer and Kovacs 1997, Laidre et al. 2002). Impacts from winter narwhal predation on Greenland halibut have been detected in Greenland halibut densities and length frequencies, particularly on the southern wintering ground (Chapter 5). Furthermore, numerous full narwhal stomachs have been found in whales harvested in winter, with most containing fresh remains from Greenland halibut (Chapter 4). In combination with the diving behavior results presented here, it appears narwhals are intensively feeding during the winter period.

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

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

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

Table 3.1. Statistics on satellite tagging results for individuals in this study. Whales in 2001 were equipped with satellite position only tags recording 'time at temperature' data and only the winter period was investigated. All other tags recorded dive depth and time at depth data using pressure transducers. Resolution of all tags was 4 m with the exception of 3961-98 and 3964-99 (6 m). The number of complete 6-hour periods collected during each season is shown. "Summer" represents tagging to 15 September, "migration" is 16 September to 31 October, and "winter" is November 1 to end of tag transmissions. Locations were received for some days where complete 6-h periods were not received; therefore, the number of days reported here does not represent tag longevity. MB=Melville Bay, ES = Eclipse Sound, and SI = Somerset Island.

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

Table 3.2. Bottom depth (m) recorded at daily good quality ARGOS locations for individuals (ID-YEAR). Data are reported as mean (SD) and range. Empty values indicate no locations were obtained for those whales during that specific time period.

Whale ID	Summer	Migration	Winter
3960-93	91 (92) 10-232	368 (390) 3-1673	784 (251) 303-1277
20167-94	360 (321) 7-970	664 (295) 37-1000	986 (181) 592-1350
6335-97	644 (136) 302-814	762 (617) 34-1916	1,485 (203) 1194-1643
20162-98	319 (233) 9-669	748 (382) 14-1989	1,321 (199) 628-1726
3961-98	419 (244) 9-711	573 (457) 37-1698	517 (77) 453-603
3964-99	422 (165) 98-668	450 (358) 33-1705	1,403 (142) 995-1769
29689-99	209 (200) 6-583	513 (240) 43-1083	-
7927-00	323 (146) 38-467	435 (358) 24-2035	2,297 (57) 2143-2355
7928-00	97 (66) 18-284	436 (373) 49-2003	-
20683-00	160 (80) 13-333	935 (623) 220-2198	-
20688-00	81 (90) 4-367	877 (757) 41-2364	940 (483) 380-1949
20689-00	42 (31) 2-91	850 (700) 22-2370	1,580 (436) 23-664
20690-00	209 (185) 5-458	953 (728) 123-2242	1,344 (554) 559-2154
7927-01	317 (161) 8-452	785 (749) 11-2291	1238 (517) 591-2348
20167-01	265 (173) 5-441	805 (776) 48-2353	2014 (341) 575-2285
20690-01	268 (163) 2-435	1033 (810) 146-2348	-
Grand Mean	265 (209) 2-970	699 (601) 3-2370	1,362 (476) 303-2355

Table 3.3. Repeated measures mixed model parameter estimates (with SE) based on an interaction model between season and locality for each of 7 depth categories (meters). A random effect of individual behavior and an effect of linear temporal autocorrelation between days (without a nugget) were included in the models. Average number of dives per day and absolute time at depth (h) in three seasons for each of three narwhal sub-populations are reported.

Average number of dives day^{-1}

	Summer			Migration			Winter		
	Eclipse	Melville	Somerset	Eclipse	Melville	Somerset	Eclipse	Melville	Somerset
0-50	159 (28)	167 (63)	149 (25)	147 (27)	165 (61)	101 (25)	116 (28)	151 (61)	59 (26)
50-100	8 (3)	11 (8)	15 (3)	7 (3)	6 (7)	10 (3)	10 (3)	13 (7)	11 (3)
100-200	4 (4)	7 (8)	8 (3)	5 (4)	4 (8)	14 (3)	10 (4)	5 (8)	19 (4)
200-400	11 (3)	14 (6)	9 (2)	7 (3)	12 (6)	20 (2)	5 (3)	3 (6)	25 (3)
400-600	11 (3)	5 (6)	6 (3)	12 (3)	6 (6)	10 (2)	3 (3)	2 (6)	12 (3)
600-800	4 (1)	10 (2)	0 (1)	7 (1)	10 (2)	2 (1)	2 (1)	4 (2)	2 (1)
>800	1 (1)	1 (2)	0 (1)	3 (1)	13 (2)	1 (1)	13 (1)	26 (3)	5 (1)

Average absolute time at depth day^{-1} (hours)

	Summer			Migration			Winter		
	Eclipse	Melville	Somerset	Eclipse	Melville	Somerset	Eclipse	Melville	Somerset
0-50	16.8 (0.8)	15.6 (1.9)	19.3 (0.7)	15.8 (0.8)	13.7 (1.8)	15.6 (0.7)	13.9 (0.8)	11.8 (1.8)	12.7 (0.8)
50-100	1.1 (0.2)	1.3 (0.4)	1.4 (0.1)	1.0 (0.2)	0.9 (0.4)	1.5 (0.1)	1.3 (0.2)	1.6 (0.4)	1.9 (0.2)
100-200	1.4 (0.2)	1.8 (0.6)	1.1 (0.2)	1.4 (0.2)	1.5 (0.5)	2.2 (0.2)	1.6 (0.2)	1.4 (0.5)	3.4 (0.2)
200-400	2.6 (0.5)	3.2 (1.3)	1.8 (.5)	2.5 (0.5)	3.2 (1.2)	3.3 (0.5)	1.7 (0.5)	2.6 (1.2)	3.6 (0.5)
400-600	1.5 (0.2)	1.0 (0.6)	0.3 (0.2)	2.0 (0.2)	1.4 (0.6)	1.0 (0.2)	1.5 (0.3)	1.4 (0.6)	1.3 (0.3)
600-800	0.4 (0.1)	0.9 (0.3)	0 (0.1)	0.9 (0.1)	1.7 (0.2)	0.2 (0.1)	1.0 (0.1)	1.8 (0.2)	0.4 (0.1)
>800	0.1 (0.1)	0.1 (0.3)	0 (0.1)	0.4 (0.1)	1.5 (0.3)	0.1 (0.1)	3.0 (0.1)	3.3 (0.3)	0.7 (0.1)

Table 3.4. Dive parameters estimated from the time budget model for individual whales in the northern and southern wintering ground. AOT_{day} is average occupancy time per day in the depth category, AOT_{dive} (AOT_{day}/# dives) is average occupancy time per dive in the depth category, and ATT_{dive} (AOT_{dive} plus the round trip transit time for a dive) is average total time for a dive to that depth category. All parameters are expressed in minutes. Standard deviations are reported in parentheses.

Depth Bin	**Northern Wintering Ground**			**Southern Wintering Ground**		
	$\mathrm{AOT_{day}}$	$\mathrm{AOT_{dive}}$	$\mathrm{ATT_{dive}}$	$\mathrm{AOT_{day}}$	$\mathrm{AOT_{dive}}$	$\mathrm{ATT_{dive}}$
0-50	677 (44)	11 (2)	11 (2)	750 (119)	6 (2)	6 (2)
50-100	30 (25)	4 (1)	6 (1)	39 (28)	5 (2)	7 (2)
100-200	111 (62)	7 (1)	10 (1)	36 (34)	6 (2)	9 (2)
200-400	157 (24)	6 (1)	11 (1)	38 (27)	8 (5)	13 (5)
400-600	64 (14)	6 (1)	13 (1)	45 (45)	8 (4)	17 (3)
600-800	9 (9)	4 (1)	14 (1)	10 (16)	5 (5)	17 (4)
>800	43 (57)	7 (1)	20 (1)	185 (40)	12 (3)	25 (2)

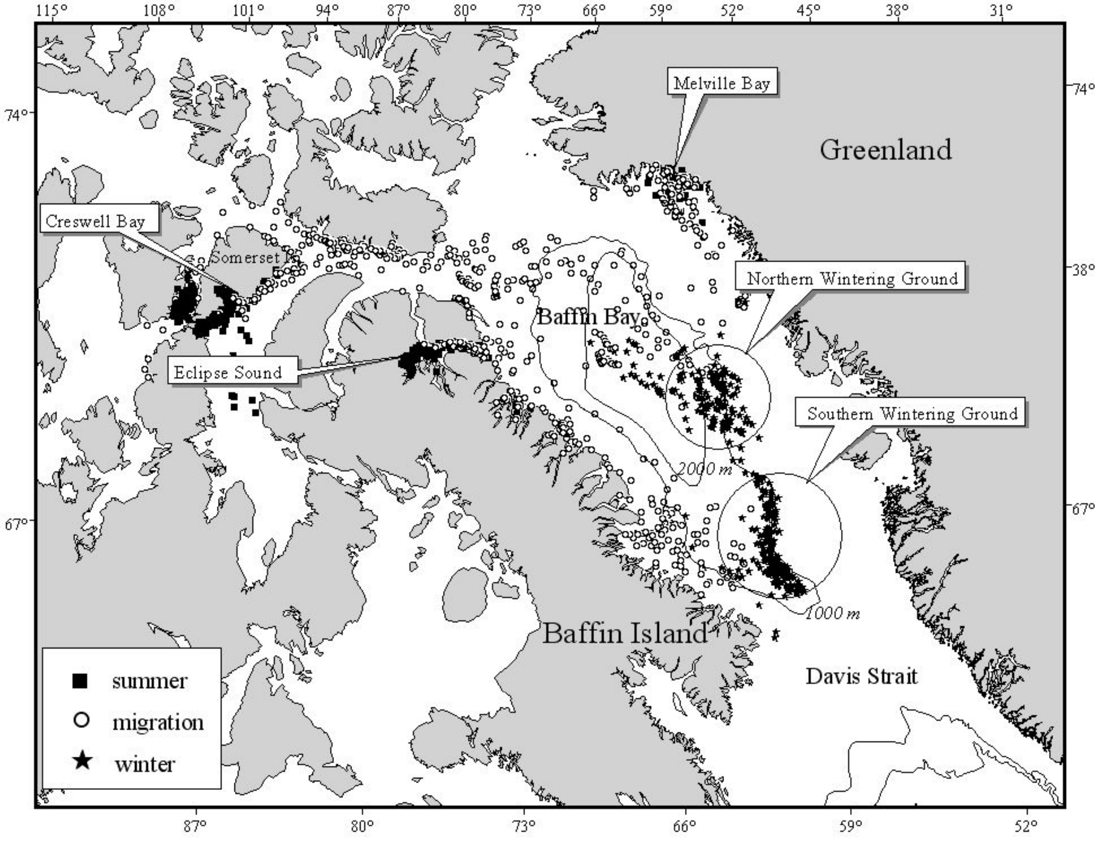


Figure 3.1. Map of the locality names, wintering grounds, and location data collected from 16 satellite tags from each of three summering grounds (Creswell Bay, Tremblay Sound and Melville Bay). Positions are classified according to the three seasons in this analysis: summer (tagging to 15 Sept), migration (16 Sept to 31 Oct), and winter (1 Nov to end of tag transmissions). Whales tagged in Tremblay Sound are from the Eclipse Sound sub-population, whales tagged in Creswell Bay are from the Somerset Island sub-population and whales tagged in Melville Bay are from the Melville Bay sub-population. The 1,000- and 2,000-m contours are shown for reference.

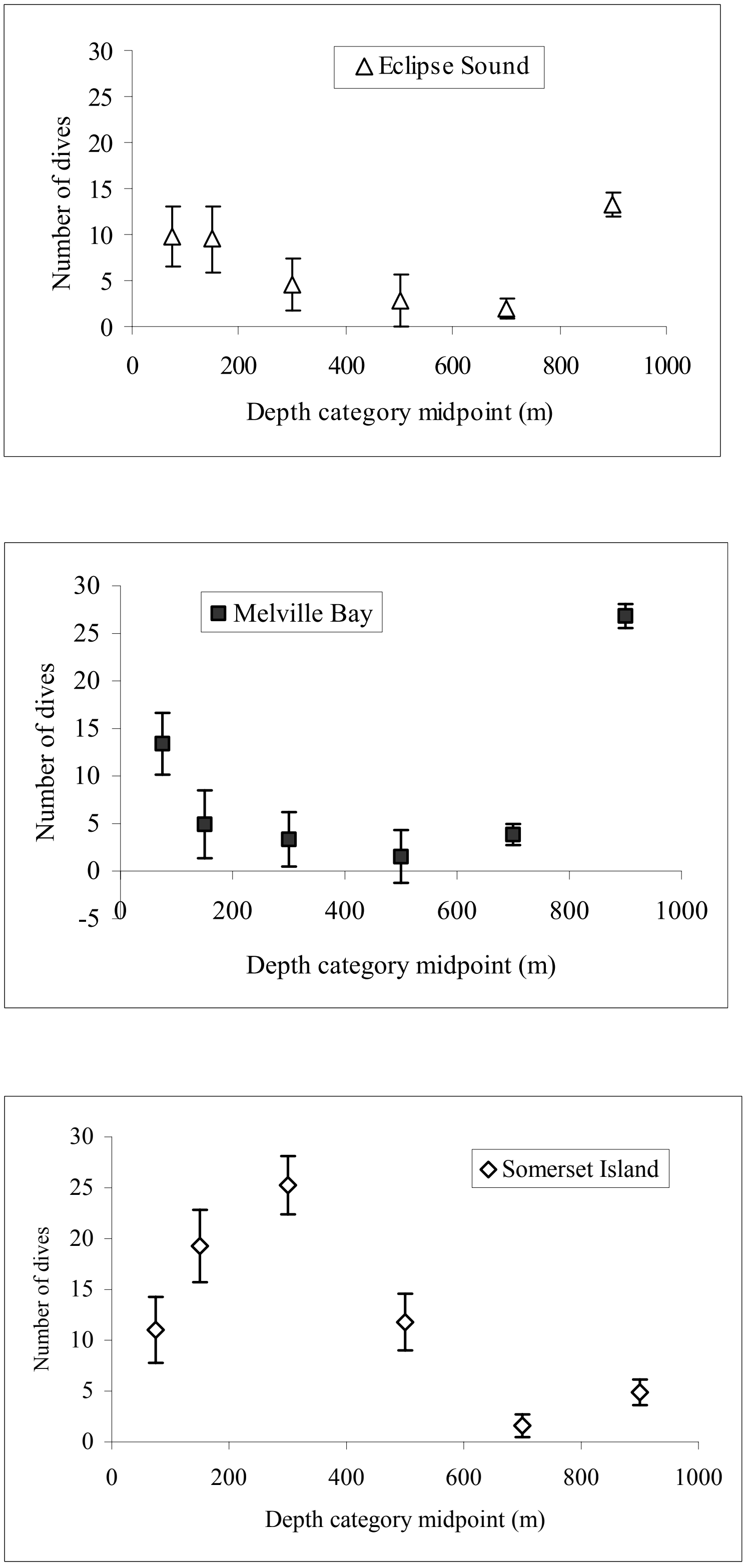


Figure 3.2. a, b, c. Parameter estimates (±SE) of average number of dives per day to different depth categories for whales tagged at 3 summering grounds, excluding surface dives (<50 m).

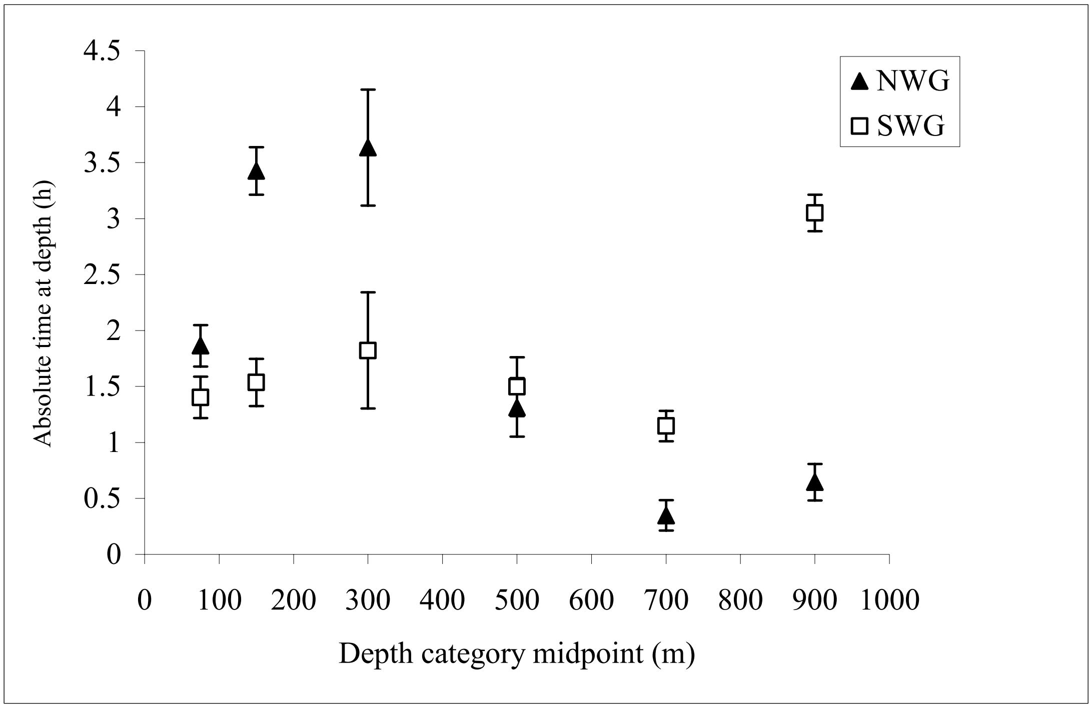


Figure 3.3. Model estimates (hours per day) of the absolute time at depth (±SE) during the winter period for whales occupying the northern and southern wintering ground, excluding time spent above 50 m. Estimates were derived from a repeated measures model on each depth bin. 'NWG' stands for Northern Wintering Ground and 'SWG' stands for Southern Wintering Ground.

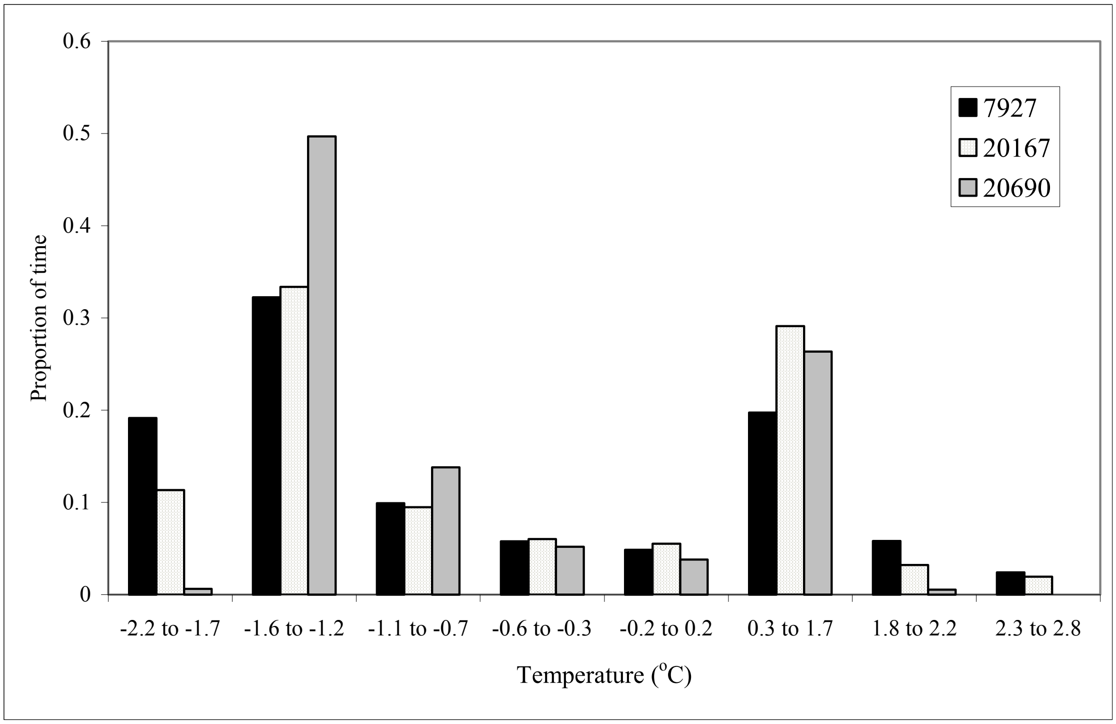


Figure 3.4. Histogram of the distribution of time-at-temperature during the winter for three whales tagged in Creswell Bay, 2001. Satellite-linked ‘time at temperature’ recorders increment temperature into categories every 10 s. Results were taken from 185 6-h periods collected after November 1 while whales occupied the wintering ground. Note, that only 2% of the time was spent at temperatures >2.3°C, and when average surface time (proportion of time spent at depths <8 m) was accounted for, travel through this category on deep dives was seldom possible.

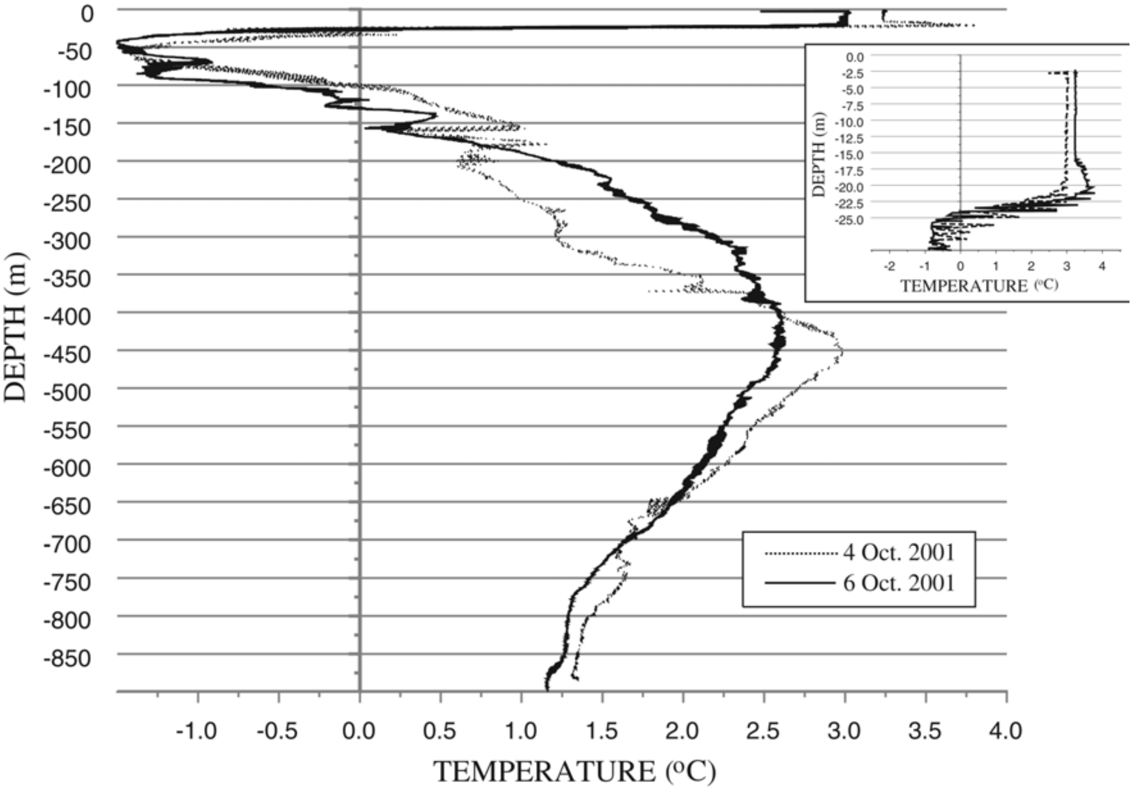


Figure 3.5. Two CTD cast profiles taken on the northern wintering ground in October 2001. Casts were taken at 72º 3.5'N, 60º 17.3'W and 71º 19.3'N, 60º 21.9'W. Inset shows detailed temperature gradient at near surface depths (<20 m). Note the thermocline (temperatures >2.3ºC) between 300-600 m, which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

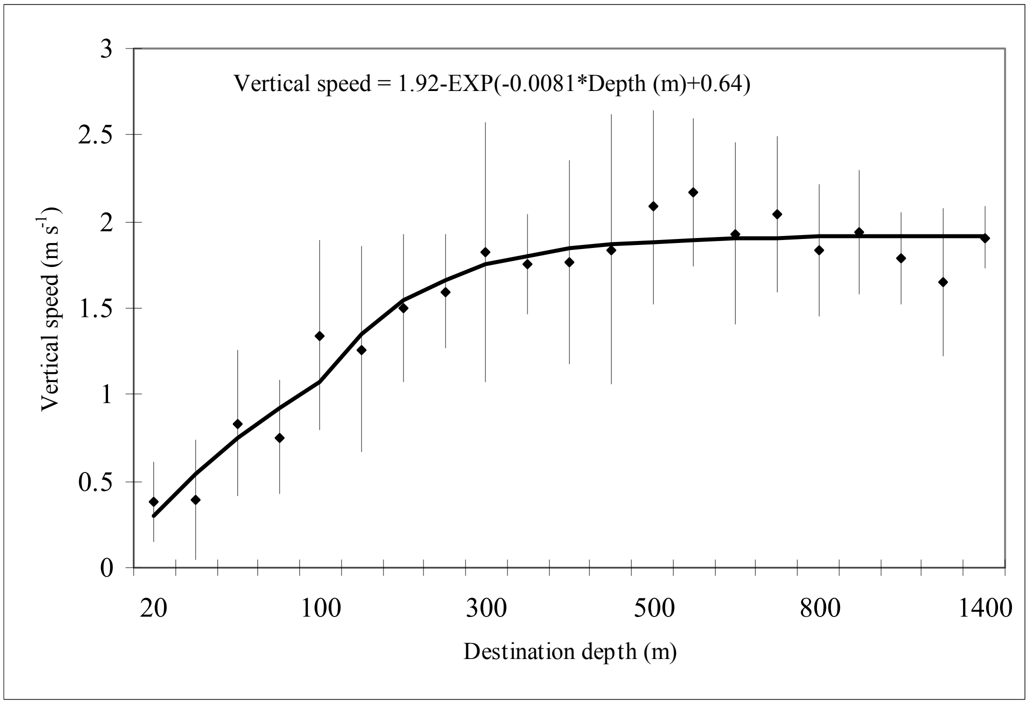


Figure 3.6. Estimates of mean vertical speed (± 1 SD) in m s^{-1} to terminal dive destination depth categories calculated for 36 narwhals tagged between 1993-2000. The exponential curve was fit to mean values for each depth category by minimizing sums of squares errors. Note chance of scale on horizontal axis.

CHAPTER 4

WINTER FEEDING BY NARWHALS

INTRODUCTION

Narwhal (*Monodon monoceros*) movements and dive behavior follow a cyclical rhythm related to seasonal changes in Arctic ice coverage and marine production. During winter months between November and April, narwhals prefer deep-water offshore areas in central Baffin Bay or northern Davis Strait. Most of what is known about their behavior and habitat preference comes from the summer period when they enter open water fjords and bays in the eastern Canadian high Arctic and Northwest Greenland (Hay and Mansfield 1989). Due to ease of accessibility and timing of harvests, narwhal dietary information has traditionally been gathered from animals taken during Inuit harvests at the summering grounds (Finley and Gibb 1982, Heide-Jørgensen 1994). This has created a strong seasonal bias to available data on the diet of the narwhal and limits information on prey selection to months between late spring and early fall, when whales are accessible to harvesters at the ice edge or in open water (Finley and Gibb 1982, Heide-Jørgensen et al. 1994).

In spring and early summer, narwhals wait along the ice edge for leads that provide access to high Arctic summering grounds. During this period they forage on Arctic cod (*Arctogadus glacialis*) and polar cod (*Boreogadus saida*) (Bradstreet et al. 1986, Welch et al. 1993, Crawford and Jorgensen 1990). Studies have suggested that the whales' presence at the ice edge is driven by migration timing rather than favorable foraging opportunities because narwhals leave the ice edge and move into summering areas as soon as ice conditions permit (Finley and Gibb 1982, Heide-Jørgensen et al. 2003a). Narwhal foraging intensity appears to be very low during summer occupation of traditional areas in fjords and bays in the high Arctic, an observation supported by many empty stomachs in summer harvests (Mansfield et al. 1975, Finley and Gibb 1982), visual behavioral observations of social interactions and behavior (Silverman 1979), and dive studies suggesting minimal foraging (Laidre et al. 2002). When narwhals move out of the summering areas in the fall, observations suggest they resume feeding, perhaps intensively, based on stomach samples and accounts of feeding frenzies (Finley and Gibb 1982). After this point, it is unknown to what extent foraging increases and if the trend continues into the winter period, as narwhals prefer offshore inaccessible habitat sampling of the late fall and winter harvests is minimal.

High arctic cetaceans (belugas, narwhals and bowhead whales) partition their annual cycle between coastal, high arctic summering grounds and southern, offshore wintering grounds. For these species, these movements are primarily due to the annual cycle of fast ice formation and recession. Fluctuation in sea ice cover may be an important factor driving feeding patterns in these species, however, little research has been done confirming this. Recently, remote satellite telemetry has revealed some insight into the behavior of narwhals during the inaccessible winter period (e.g. Heide-Jørgensen and Dietz 1995, Dietz et al. 2001, Heide-Jørgensen et al. 2002a). From November through April, approximately 50,000 narwhals (Innes et al. 2002) remain in localized areas (25,000 km^2) in central Baffin Bay (Heide-Jørgensen et al. 2003a). During this period, they display intense deep-dive behavior, making many dives (up to16 dives 24h^{-1}) to the bottom each day (depths 800 to >1,500 m) (Laidre et al. 2003). These focused dive patterns have been inferred to be foraging behavior and winter diet has been assumed to be primarily benthic or mid-water prey species, such as Greenland halibut (*Reinhardtius hippoglossoides*) and *Gonatus* squid spp. (Finley and Gibb 1982, Heide-Jørgensen et al. 1994, Heide-Jørgensen et al. 2003a). Evidence that Greenland halibut biomass, densities, and length distributions in some offshore areas are impacted by narwhal predation supports these assumptions and suggests narwhal predation in Baffin Bay has a large impact on the ecosystem (Chapter 5).

Given that re-constructing the diet of deep-diving, offshore cetaceans is difficult and often elucidated through stomachs collected from stranded animals or bycatch (Santos et al. 1999, Santos et al. 2001b), the narwhal provides a unique opportunity in that it is a deep-diving odontocete harvested throughout much of its range in the eastern Canadian high Arctic and West Greenland. One of the only methods of gaining insight on winter feeding of narwhals is to utilize the occurrence of approximately 3,000 narwhals in the Disko Bay region, West Greenland, the only predictable coastal winter occurrence of narwhals worldwide (Heide-Jørgensen and Acquarone 2002) (Figure 4.1). On average 154 narwhals (SD 54, range 75-268) are taken annually between the months of December and April by local hunters in this region (catch statistics between 1993-2001) with 41% of the catch female whales (Heide-Jørgensen, unpublished data). In this study, stomach samples were collected from narwhals harvested during late fall and winter months. Results were used to contrast feeding choice and intensity to stomach contents from narwhals harvested on several summering grounds throughout their range since 1993. This information was used to provide a comprehensive review of the seasonal feeding ecology of narwhals in the Baffin Bay and adjacent waters.

METHODS

Whole stomachs were collected by Inuit hunters or biologists in West Greenland and in the eastern Canadian high Arctic. All stomachs were examined immediately in the field, either shortly after the death of the whale or after a 1 to 5 month period in a freezer. Stomachs were taken from summer localities in Canada in Eclipse Sound in August 1999 (n=8), in West Greenland near Inglefield Bredning in August 2002-2003 (n=8), and in West Greenland in Melville Bay in August 2002 (n=5) (Figure 4.1). Narwhals were taken in open water, close to shore (<10 km) at all summer localities. Stomachs were taken in fall near Uummannaq, West Greenland in November 1993 (n=51) and winter stomachs (n=22) were collected from hunters in the vicinity of Disko Bay, West Greenland between December 2002 and April 2003. Whales in Disko Bay were harvested in water depths up to 800 m as far as 20 km from shore, near the island of Imerisoq (Figure 4.1).

Frozen stomachs were thawed overnight for analysis and the entire stomach was weighed, opened and the content weighed separately. Most prey items were obtained from the forestomach, although the main and pyloric stomachs were also examined, if present. Fleshy pieces were set aside and hard parts (otoliths, vertebrae, crustacean skeletons or squid beaks) were rinsed with water in fine mesh sieves and dried. Identification of prey was almost entirely based on the examination of otoliths and bones from fish, crustacean skeletons, and chitinous lower beaks from cephalopods. Items were identified based on comparison with material from past stomach content analyses and literature references. In the case of recent meals (where some prey items were not yet digested) body sizes were measured (i.e., *Pandalus* shrimp). Otoliths collected from polar cod and Arctic cod were not distinguished and were pooled into a single category.

Almost all stomachs contain some of hard parts from prey items, however, this occurrence is not necessarily indicative of recent ingestion since hard parts can be retained for long periods of time. Stomachs in this study were classified as containing 'old' or 'fresh' remains. Stomachs were classified as having 'old' remains when a few hard parts were found tucked in the folds of the stomach wall, evidently there for some length of time, with no presence of flesh or muscle suggesting fresh ingestion. Stomachs were classified as having 'fresh' remains when evidence of recent (within 24 hours) feeding was found based on the occurrence of intact fish muscle, skulls, large numbers of fish bones, intact crustacean skeletons, or soft muscle attached to squid beaks. All prey items were identified and, if possible, stomachs were classified based on the dominant prey species present. A sub-sample of representative squid beaks and otoliths was collected from each stomach during the winter period. Otoliths and lower rostral length (LRL) of squid beaks was measured to estimate the range of sizes of prey items. Pristine otoliths found inside fish skulls (classified as undigested) were extracted and separated from those found outside skulls (classified as digested) and sizes were compared using standard t-tests. A digestion correction was calculated to adjust fish size estimates predicted from measuring loose otoliths (subjected to stomach acids). Fish or squid standard length calculations were based on measurements of pristine otoliths or LRL and standard published regression equations (Clarke 1962, Härkönen 1986).

RESULTS

Summer

Intensive feeding was not found in any locality during the summer period. Over half of the sampled stomachs from all localities were completely empty and only <15% contained fresh remains or fleshy material. Stomachs collected in Eclipse Sound, Canada in 1999 (n=8) were sampled from whales harvested between 12-23 August. Stomachs were collected from 5 females and 3 males ranging in size from 282-456 cm (standard length). Six of the stomachs were completely empty (4 F and 2 M) and two contained a few (<100) squid beaks and polar cod otoliths, with no soft parts (Table 4.1).

Stomachs sampled in Melville Bay (n=5) in August 2002 were either completely empty or contained only a few *Gonatus* squid beaks or otoliths, without fresh muscle or flesh. Prey items from Melville Bay included unidentified *Gonatus* squid spp., polar cod, Arctic cod, and *Pandalus* (Table 4.1). Mean mass of the wet weight of contents was 0.5 kg for this area, with the content weight from some stomachs nearly negligible. No information on size or sex of narwhals was available with these stomachs.

Stomachs collected in Inglefield Bredning in August 2002 and 2003 were from whales harvested in inner parts of the Inglefield Bredning fjord in mid-August (4 males, 2 females, and 2 juveniles). Average wet weight of the stomach contents in this area from 2003 was <1 kg. Five of the eight stomachs sampled from Inglefield Bredning were empty. Of the 3 that contained material (from 2 M and 1 F, >4 m length), fresh remains were found from Arctic and polar cod. Other prey species found sparsely in Inglefield Bredning included Greenland halibut (6-7 mm otoliths), *Pandalus* shrimp and *Gonatus*. This was the only summer locality were evidence of recent feeding was observed.

Late fall

Stomachs (n=51) were collected during the annual narwhal harvest in Uummannaq, West Greenland, between 3-18 November 1993. Two-liter samples of stomach contents were taken from all animals >200 cm in standard length. Seventeen females and 35 males were sampled, during this period ranging in standard length from 205-490 cm. The squid *Gonatus fabricii* constituted 100% of the diet of whales in this area (Table 4.1) and all stomachs had fresh remains. In addition to hundreds of eye lenses and squid beaks with muscle attached, several intact specimens of *G. fabricii* were found in stomachs, suggesting recent ingestion by all whales. No differences were found between male and female stomach contents. Out of 51 stomachs examined, only one fish bone (unidentified) was found.

Winter

All stomachs taken from whales harvested during winter in Disko Bay 2002-03 (samples spanning the months of December-April) were full of fleshy soft parts from recently ingested prey items. The mean mass of the wet weight of stomach contents (n= 22) was 5.4 kg (SD 6.5, range 0.5-25). No sex or age information was collected from whales harvested during this period. The most frequent prey items were Greenland halibut or *G. fabricii*, and often only a single prey item dominated the contents of the stomach. Forty-five percent (n=10) of the stomachs were entirely full of fresh flesh from Greenland halibut, with insignificant amounts of *G. fabricii* or *Pandalus* shrimp that could have been of secondary origin. Stomachs dominated by Greenland halibut contained large amounts of greasy white lipid. Greenland halibut dominated the five largest and heaviest stomachs (16 to >30 kg) but was also dominant in some smaller stomachs (<10 kg). *G. fabricii* and *Pandalus* were only found in stomachs <11 kg, and the majority of which were 5 kg. 36% of the stomachs were dominated by *G. fabricii* (n=8) and it was the second most important prey item in the winter sample (based on dominant prey).

Two stomachs from Disko Bay (<10% of the sample) were dominated by *Pandalus* shrimp, approximately 80-85 mm long. Of these, two of the *G. fabricii* dominated stomachs and one of the *Pandalus*-dominated stomachs also contained many Greenland halibut otoliths. Two stomachs contained mixed prey items and could not be classified as dominant for a single species: one stomach contained fresh remains from 3 wolffish (*Anarhichas lupus* and *A. minor*), rocks, and 2 skate egg sacks (probably *Raja sp.*) together with <50 *G. fabricii* beaks, and another stomach contained evidence of very large prey items of Greenland halibut, *G. fabricii,* and several rocks.

There was a wide range of size classes of *G. fabricii* found in each stomach suggesting ingestion of both juveniles and spawning adults. The LRL measurements were on average 3.3 mm (SD 0.85, range 1.7-5.7). Based on regression equations provided for *Gonatus* spp. in Clarke (1962), this corresponded to a mean wet weight (g) of 35.6 (SD 31.1, range 3.0 –167.9) and mean mantle lengths (mm) of 95.1 (SD 36.2, range 4.4-176.3). Greenland halibut otoliths (n=253) ranged in size from 3 to 10 mm, and overall average size for all otoliths pooled was 6.2 mm (SD 1.5). Undigested Greenland halibut otoliths (n=141) and digested otoliths (n=112) were obtained from 5 narwhal stomachs. When otoliths from the two categories were pooled for the five stomachs, undigested otoliths were significantly larger (mean 6.9 mm, SD 1.5) than digested otoliths (mean 5.4 mm, SD 1.1) ($p<0.001$). Within each individual stomach, three out of four had significantly larger undigested Greenland halibut otoliths than digested Greenland halibut otoliths ($p<0.001$) (Table 4.2). Average fish length and mass, calculated from undigested otoliths based on power functions provided by Härkönen (1986), was approximately 36 cm (SD 9, range 9 to 55 cm) and 430 g (SD 275, range 275 g to 1.4 kg). Using digested otoliths underestimated the length and mass of Greenland halibut by approximately 75% and 40%, respectively.

DISCUSSION

Seasonal variation in prey selection and feeding intensity

This study reports generalized findings of stomach contents of 94 narwhals taken between 1993-2003. The observations of prey species, feeding intensity and frequency, and prey size, combined with results from previous studies, provide a clear picture of the seasonal feeding habits of the narwhal (Table 4.1). Overall, the narwhal appears to vary food intake seasonally, a behavioral trait linked to its annual pattern of migration and focal occupancy periods in summer and winter.

Stomachs were largely empty during the summer period and <15% of those examined contained fresh remains. This finding is supported by multiple previous studies where over 244 narwhal stomachs were examined during summer. Many of these were completely empty and very few were found to contain fresh remains (Vibe 1950, Mansfield et al. 1975, Meldgaard and Kapel 1981, Finley and Gibb 1982, Hay 1984, Weaver and Walker 1988, Heide-Jørgensen et al. 1994, Heide-Jørgensen and Dietz 1995) (Table 4.1). In this study, the summer period in Inglefield Bredning was the only period where stomachs contained some fresh remains from Arctic or polar cod. Arctic and polar cod have been reported to be important components of the summer diet of the narwhal and other top Arctic carnivores in coastal northern areas and at the ice edge in Canada and Greenland (Vibe 1950, Finley and Gibb 1982, Bradstreet et al. 1986, Crawford and Jorgensen 1990, Heide-Jørgensen et al. 1994). Of the summer localities, feeding intensity in Inglefield Bredning may be slightly higher than from whales summering in the Canadian high Arctic. Note, however over half of the sampled stomachs in this region were empty. The occurrence of polar and Arctic cod (fresh remains or otoliths) quickly declined or was absent in all stomachs sampled in fall and winter suggesting these species are seasonally important or are taken opportunistically, given their common occurrence at the ice edge (Table 4.2). Despite the large schools of Arctic and polar cod that widely occur on the high Arctic summering grounds (Bradstreet et al. 1986, Crawford and Jorgensen 1990, Welch et al. 1992, Crawford and Jorgensen 1993, Welch et al. 1993), they do not appear to intensively utilized by narwhals food during summer.

Gonatus squid remains were found in all seasons and in all localities, positively identified as 100% *G. fabricii* in late fall and winter stomachs. Some summer samples of *Gonatus* were unidentified, however were also likely *G. fabricii. T*his squid is by far the most abundant squid in the offshore Arctic and sub-Arctic waters of the northern Atlantic (Piatkowski and Wieland 1993). *Gonatus* are distributed throughout Baffin Bay and coastal West Greenland both at deep and mid-water depths (Kristensen 1984). *G. fabricii* adults (>30 to 35 mm pen length) are common at mid-water and on the bottom, where as juveniles (6-35 mm pen length) occupy the epipelagic zone (Kristensen 1984, Piatkowski and Wieland 1993). Squid found in the diet of narwhals taken in autumn in Uummannaq are consistent with traditional knowledge reporting large schools of *G. fabricii* squid arriving in the area to spawn. Traditional knowledge, harvest records, and biologists observations indicate narwhals arrive predictably in this area in the beginning of November and remain in the region for 2-3 weeks foraging on *G. fabricii*. The whales depart in late November, when spawning is over and sea ice forms, to an unknown their winter destination. The predictable spawning of *G. fabricii* in the Uummannaq area and coincident narwhal arrival has supplied an annual catch of up to 1,000 whales in this region (Heide-Jørgensen 1994).

The northern shrimp, *Pandalus borealis*, was found in some stomachs from Melville Bay in summer as well as in some full stomachs in Disko Bay in winter. *Pandalus* occur widely along the West Greenland coast as far north at Melville Bay and are, in economic terms, the most important fishery species in Greenland. Odd prey items were found in one stomach from Disko Bay, including the first report of wolfish in the narwhal diet, as well as skate or ray eggs (also reported in narwhal stomachs in Pond Inlet by Finley and Gibb (1982) and Weaver and Walker (1988)). Rocks found in several winter stomachs suggest benthic feeding along the sea floor.

Greenland halibut dominated the winter stomach contents from Disko Bay and was often the only prey item identified in a completely full stomach. The species was also occasionally detected in summer stomachs in Inglefield Bredning, however not in the same abundance. Greenland halibut are distributed in deep waters of Baffin Bay and coastal fjords >500 m. The greatest densities occur between 800-1200 m in central Baffin Bay (Jørgensen 2002), the same location at which the narwhal wintering grounds are located and depths at which narwhals have been observed to repetitively dive. Greenland halibut are an important target for commercial fisheries in West Greenland, and renewed interest in an offshore fishery recently has developed in Canada (Treble et al. 2000, Treble and Jørgensen 2002). Despite the possible under representation of Greenland halibut due to partial or full digestion of otoliths, this species appears to be the dominant food item on the wintering ground. On a caloric basis, Greenland halibut are lipid-rich and contain higher energy content than Arctic or polar cod (Lawson et al. 1998). During stomach examination this high oil content was apparent in stomachs with recent halibut meals. The benefit of making deep dives to the bottom to prey on Greenland halibut is evident from the gain in energy content from this lipid-rich source.

The frequency of occurrence of fresh prey items in narwhal stomachs was used to determine how recently and to what degree feeding activity had occurred. The occurrence of full stomachs and fresh remains was, by far, most prominent during the late fall and winter period. None of the stomachs examined on any of the summering grounds showed a similar amount of prey consumption. This is in agreement with previous summer studies (Finley and Gibb 1982), some dating 40 years back, where Mansfield et al. (1975) noted “few specimens contained food” of 62 narwhal stomachs sampled in August in the early 1960’s. Average content wet weight in summer was 1/5th of that found in winter (<1 kg in Inglefield Bredning vs. 5.4 kg in Disko Bay), also similar to that found by Heide-Jørgensen et al. (1994) of 1.8 kg wet weight of contents for 35 summer stomachs. Although assessing the relevance of empty stomachs is difficult, given the frequency with which they were found in summer in this study and previous studies, it appears food consumption is at a minimum during the summer high Arctic period. This study provides the first evidence that the bulk of the energy gain is obtained from foraging efforts in the late fall and on the wintering grounds in West Greenland and central Baffin Bay/Davis Strait. This supports quantitative and spatial evidence of Greenland halibut predation in deep-water Baffin Bay (Chapter 5) and confirms the importance of the wintering grounds to the sub-populations.

Biases and shortcomings

Stomachs sampled from recently harvested animals, rather than stranded animals or bycatch, provide a non-biased picture of dietary preferences and food consumption of the healthy population. It is incorrect to assume that stomachs sampled from stranded animals, commonly unhealthy or in foreign habitat prior to stranding, are representative of population level feeding habits (e.g., a narwhal found outside its natural range may not contain any of the prey items reported here). It is optimal to sample stomachs from species with pelagic occurrence where predation occurs (see also Ohizumi et al. 2003). It has not been possible sample the narwhals at their offshore wintering grounds in the heavy pack ice and here we have used samples from a coastal wintering area as a proxy for offshore diet preference and intensity. It seems reasonable, based on diving behavior and residence times, to assume similar levels of feeding as those animals sampled in coastal areas.

Potential sources of bias such as retention time in the stomach, digestion, and secondary ingestion, are generally prevalent in stomach content studies. The narwhal stomach is unique in that it has many convoluted, fingerlike-folds along the inner lining that easily catch and retain hard parts such as squid beaks (Woodhead and Gray 1889). Although cephalopod flesh is digested more rapidly than fish muscle (Santos et al. 2001a), the beaks are often trapped and accumulate in the folds of the stomach remaining undigested for long periods of time (Santos et al. 1999, Santos et al. 2001a). Fresh *Gonatus* was found only in the narwhal stomachs in fall and winter, and in summer, beaks were the only evidence found that narwhals had at some unknown occasion taken *Gonatus*. The fragility and quick digestion of Greenland halibut otoliths likely contributed to the underestimate of this species. This was clear upon the large discrepancy between digested Greenland halibut otoliths and those still in the fish skulls. The underestimation of Greenland halibut is further pronounced as it is by far the largest size prey consumed, and one halibut (therefore two otolith hard parts) can easily be the caloric equivalent of hundreds of *Gonatus* or *Pandalus*. Arctic and polar cod otoliths are much more robust and may remain in the convoluted folds of the narwhal stomach for much longer periods. *Pandalus* shrimp is the primary prey of Greenland halibut (Jørgensen 1997a), and the *Pandalus* telsons found in narwhal stomachs could have been secondary prey items.

Sex and body size measurements were not taken by hunters for some of the narwhals in this study and consequently, sex-based dietary comparisons were not possible. Finley and Gibb (1982) reported no sex or age group differences between the diet, numbers of prey items, or prey sizes taken by narwhals in Pond Inlet, Canada. Where sex was available for samples in this study (summer and fall), no differences were found between stomach contents of males and females. No apparent differences in deep-diving capabilities have been detected between males and females so dietary limitations are likely not related to physiological limitations in reaching certain depths (Laidre et al. 2003). In the case of harvest bias, records from the winter in Disko Bay between 1990 and 1994 report 41% of the harvest was females (Heide-Jørgensen, unpublished data), indicating little bias, if any, in the hunters selection of whales by sex. The Greenland harvest is not necessarily biased towards males with tusks because hunters make an larger profit from selling muktuk. Consequently the proportion of female whales in this winter sample taken from the harvest is likely not underrepresented.

Prey selection

There is a low variety of prey species comprising the diet of the narwhal. Stomachs were dominated by no more than five primary prey species: polar cod, Arctic cod, *G. fabricii*, *Pandalus* shrimp, and Greenland halibut. This is relatively surprising given that a large number and diversity of prey species have been found in cetacean stomachs, particularly odontocetes with a deep-diving ability (Santos et al. 2001a, Santos et al. 2001b, Walker et al. 2002, McLeod et al. 2003, Whitehead et al. 2003). Whitehead *et al.* (2003) postulate that diversity of cephalopods in the diet, particularly for deep diving marine mammals, may be driven by species' movement patterns. They suggest species traveling widely across ocean basins, such as the sperm whale (*Physeter macrocephalus*), have a more diverse diet than those making smaller scale movements (4 km/day assumed, perhaps incorrectly, for the northern bottlenose whale, *Hyperoodon ampullatus*). Given that the narwhal travels over 3,000 km between summering and wintering grounds during its annual migration, and has displacement distances of on average 43-77 km/day (Dietz et al. 2001, Heide-Jørgensen et al. 2003a), horizontal movements are far beyond that reported for the wide-ranging sperm whale (26 km/day) (Whitehead et al. 2003). An alternate explanation of the low diversity in the diet of the narwhal is rather that the species annual cycle is restricted to the high Arctic ecosystem. In high latitude ecosystems, prey species are often found in high densities but low faunal diversities and consequently, narwhals may encounter lower species diversity throughout their lifetime in the Arctic. Another item of interest in terms of prey choice is the large size range of of prey taken by narwhals. Prey items in this study ranged from 30 g Pandalus shrimp to 430 g Greenland halibut. It is likely narwhals successfully forage on small prey items because they exploit high densities or swarms. In the case of Greenland halibut, extremely high densities are not as important as fewer prey items, numerically speaking, can satisfy energetic needs.

Importance of winter feeding grounds

High arctic cetaceans partition their annual cycle between coastal, high arctic summering grounds and southern, offshore wintering grounds. For these species, seasonal movements are primarily due to the annual cycle of fast ice formation and recession. Consequently, the 3-5 month occupancy in the summering and winter areas is intersected by periods of long-distance migration, either in front of the forming ice or following the receding ice edge. Narwhals display high site fidelity to summer and winter areas (Heide-Jørgensen et al. 2003a). Specifically in the case of the winter period, whales return annually to areas with extremely dense, dangerous pack ice despite the high risk of ice entrapments (Heide-Jørgensen et al. 2002b, Siegstad and Heide-Jørgensen 1994, Chapter 7). Given remote telemetry observations of repetitive deep diving, together with evidence of impacts on Greenland halibut stocks (Chapter 3) the information provided in this study suggests winter feeding may partially explain the high fidelity to the wintering grounds. It is entirely possible that whales are driven by a need to reach predictable prey, despite dense consolidated pack ice. Adult and juvenile survival on the migration north or the summering grounds, as well as female condition during calving and nursing in late spring/early summer, may depend on food intake during the winter period. In light of recently reported increases in sea ice concentration and extent in Baffin Bay (Stern and Heide-Jørgensen 2003, Chapter 8), reliance on a single prey source especially in restricted habitat, may leave a population highly vulnerable to perturbations in climate (IWC 1997).

Two other high Arctic cetaceans display similar timing of movements and feeding intensity. The beluga or white whale (*Delphinapterus leucas*) undertakes similar long distance migrations to winter feeding grounds in West Greenland (Heide-Jørgensen et al. 2003b). Belugas summer in the eastern Canadian high Arctic and apparently feed little during the July and August estuarine period (Koski and Davis 1994). During their migration out of the summering grounds, belugas increase their foraging intensity taking both polar and Arctic cod in feeding frenzies. After the arrival on the wintering grounds in coastal West Greenland, where they are reported to arrive very thin, they feed heavily on cod (*Gadus morhua*), redfish (*Sebastes* spp.), wolfish, and Greenland halibut and depart heavier in spring (Degerbøl and Mielsen 1930, Heide-Jørgensen and Teilmann 1994). At least 15% of the population of belugas that summer in the Canadian high Arctic winters in West Greenland (Heide-Jørgensen et al. 2003b). The rest of the population winters in the North Water Polynya, where nothing is known about their feeding behavior or prey choice. The high Artic mysticete, the bowhead whale (*Balaena mysticetus*), also utilizes the West Greenland region beginning in early spring (February and March) (Eschricht and Reinhardt 1861). Bowhead whales arrive predictably along the West Greenland coast, probably from offshore areas where production and feeding opportunities are less available. Here they take advantage of the rich abundance of zooplankton through May before departing north for Canadian waters (Madsen et al. 2001, Heide-Jørgensen et al. 2003c).

The inflow of warm Atlantic water along the West Greenland coast has a large influence on the ecosystem productivity and composition. Various oceanographic factors driving the ecosystem structure contribute to this the production, on which these high Arctic cetaceans depend and thrive. Given the reliable annual winter occurrence of the three high Arctic cetaceans in West Greenland (Heide-Jørgensen and Acquarone 2002) and observations of foraging intensity during the period of occupancy, the West Greenland ecosystem appears to be a critical region providing an abundance of dependable resources (Heide-Jørgensen and Laidre, In Press).

The high Arctic cetaceans are not the only marine mammals that take advantage of the high production in West Greenland. When the high Arctic cetaceans move north in spring with the receding ice, marine mammals from winter breeding grounds at latitudes south of Greenland move into the rich waters to feed through the summer and fall. This includes humpback whales (*Megaptera novaengliae*) (Stevick et al. 2003), minke whales (*Balaenoptera acutorostrata*) (Horwood 1990), harbour porpoises (*Phocena phocena*) (Teilman and Dietz 1998), fin whales (*Balaenoptera physalus*) (Larsen 1995), sei whales (*Balaenoptera borealis*) (Kapel 1985), sperm whales, blue whales (*Balaenoptera musculus*), pilot whales (*Globicephala melaena*), bottlenose whales (Kapel and Larsen 1983), harp seals (*Phoca groenlandica*) (Sergeant 1976, Sergeant 1991, Kapel 2000), and hooded seals (*Cystophora cristata*) (Kapel 2000). These species utilize a broad range of the trophic food web from zooplankton to pelagic forage fish to benthic prey. The seasonality of their utilization essentially creates two categories of marine predators using the area: those found during winter and those utilizing the area during summer.

The cyclicity of extensive movements between productive high latitude feeding grounds in summer and lower latitude winter calving or breeding grounds has been documented for several cetacean species in the northern and southern hemispheres (Lockyer and Brown 1981). The populations undertaking these north-south migrations tend to have high site fidelity to summering and wintering areas and tend to display the same behavioral patterns: little to no feeding on the calving or breeding grounds in winter and accumulation of most energy gain in summer. The timing of the utilization of the West Greenland ecosystem appears to be reversed for the high Arctic cetaceans (narwhal, beluga and bowhead whale). The winter period used for intense feeding is likely an adaptation to the reduced productivity at the high Arctic summering areas and life history strategies favoring Arctic success. On a large time scale, the periods of glaciation have shaped the overall migration patterns of high Arctic cetaceans however on smaller time scales, the annual formation and recession of sea ice undoubtedly governs both the ecosystem production and the whale's access to prey.

Table 4.1. Seasonal percentage occurrence of the most common prey items in narwhal stomachs. Results from previously published studies are included for comparison. N is the number of narwhal stomachs examined in each study. The "% of stomachs with fresh remains" column was quantified based on the proportion of stomachs containing fresh flesh from prey items indicating recent feeding. Some studies did not quantify the percent occurrence of each prey species and an "x" simply indicates which species were found but not enumerated. "Na" indicates information is not available. Prey species are PAC = Polar and Arctic cod, GHL = Greenland halibut, GO = *Gonatus* spp., and PA = *Pandalus* spp.

Season and habitat	Locality	Data Source[a]	N	% stomachs with fresh remains	PAC	GHL	GO	PA	Mean wet content weight (kg)
Early summer/ ice edge	Pond Inlet	5	35	na	x	x	x		
		6	33	>50%	x		x		
Summer/ open water	Inglefield Bredning	1	8	50	88	13	38	0	<1
		8	35	na	75	0	20		1.8
		2	na	na	x	x			na
	Melville Bay	1	5	0	60	0	80	20	<0.5
		9	3	0	x			x	na
		4	1	0	x		x		na
	Pond Inlet/Eclipse Sound	1	8	0	13	0	25	0	<0.5
		3	62	0	21				
		5	38	na	x	x	x		
		6	58	0	x		x		
		7	47	na	?	x	x		
Fall/ new ice	Uummannaq	1	51	100	0%	0	100	0	na
Winter/ pack ice	Disko Bay	1	22	100	5	64	64	31	5.4

References: [1]Present Study, [2]Vibe (1950), [3]Mansfield et al. 1975, [4]Meldgaard and Kapel (1981), [5]Finley and Gibb (1982), [6]Hay (1984), [7]Weaver and Walker (1988), [8]Heide-Jørgensen et al. 1994, [9]Heide-Jørgensen and Dietz (1995).

Table 4.2. Five narwhal stomachs collected during winter in Disko Bay, West Greenland 2002-03 where sizes of digested (loose inside stomach) and undigested (removed directly from skulls) Greenland halibut otoliths were compared. Mean otoliths size, estimated fish length (with SD), and significance levels from t-tests comparing digested and undigested otoliths lengths are reported. Size of Greenland halibut was predicted based on the equation taken from Härkönen (1986). "ns" indicates non-significant result.

ID	N undigested otoliths	N digested otoliths	Undigested Otolith size (mm)	Digested Otolith size (mm)	Undigested fish length (cm)	Digested fish length (cm)	P-value
1	24	16	7.25 (0.9)	5.77 (0.9)	38 (5)	29 (5)	<0.001
2	30	27	4.65 (1.2)	5.19 (1.1)	23 (7)	26 (6)	ns
3	46	27	7.54 (0.8)	5.74 (1.0)	40 (5)	29 (6)	<0.001
4	33	36	7.47 (1.0)	5.01 (0.9)	39 (6)	25 (5)	<0.001
5	7	5	7.56 (1.2)	6.66 (1.5)	40 (7)	35 (9)	ns

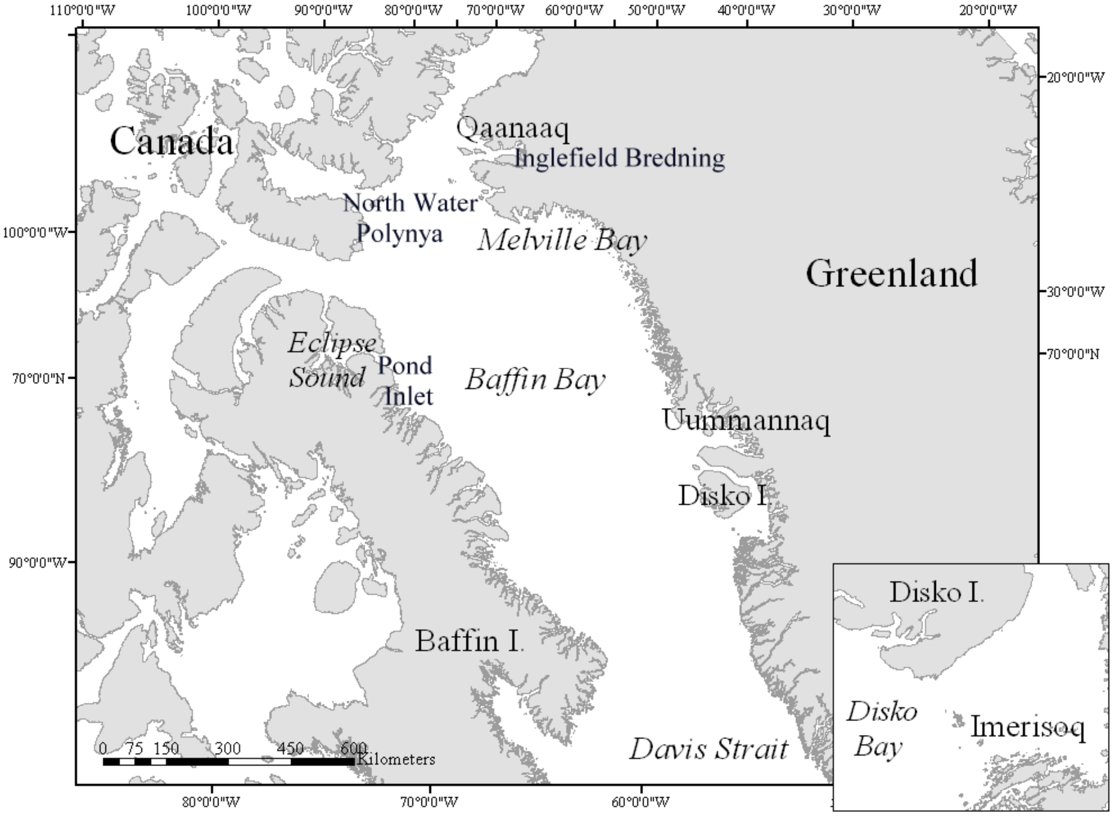


Figure 4.1. Map of localities mentioned in text. Inset shows close-up of Disko Bay winter region where narwhals were harvested.

CHAPTER 5

DEEP-OCEAN PREDATION BY NARWHALS

INTRODUCTION

Most marine mammals are carnivores that function as apex predators in the marine ecosystem and many prey species consumed by marine mammals are likely to be important target species of commercial fisheries or linked to such species though the food web (Kenney et al. 1995). Trophic interactions linking marine mammals and the marine food web have been an important conservation issue for decades, involving a myriad of species from sea otters and abalone in California, to fur seals and fisheries in the Bering Sea (Beddington et al 1985). Fish stock depletion, predation impacts on fish catches, increasing efficiency of fishing operations, and the development of new fisheries have been a primary factor causing conflicts over interactions with marine mammals and seabirds. Previously unexploited, deep oceanic areas are currently becoming the target of modern fishing operations and are introducing new challenges in terms of understanding functional relationships between fisheries and top marine predators. One potential conflict is the emerging deep-water fishery for Greenland halibut (*Reinhardtius hippoglossoides*) in Arctic waters of Baffin Bay and Davis Strait. This fishery will operate in Arctic waters shared with deep-diving narwhals that feed heavily in dense pack ice on Greenland halibut.

Narwhals (*Monodon monoceros*) in Canada and West Greenland make long distance migrations each year between northern summering grounds and southern wintering grounds (Dietz et al. 2001, Heide-Jørgensen et al. 2003a). The timing and extent of the fall narwhal migration is due to forming fast ice in their summer habitat, and consequently all sub-populations move south and winter in Baffin Bay and northern Davis Strait for at least 5 months of the year (Figure 5.1). On the wintering grounds, large numbers of whales are concentrated in small regions over water depths up to 2,300 m. There appear to be differences in foraging behavior between different wintering grounds with different bathymetry (Laidre et al. 2003). Narwhals from Melville Bay, West Greenland and Eclipse Sound, Canada share a wintering ground in southern Baffin Bay. Whales in this area make significantly more deep dives and spend significantly more time at depths $\geq$800 m than the sub-population of narwhals from Somerset Island, Canada occupying a wintering ground farther north. These differences in diving behavior have been proposed to indicate differences in local prey availability or foraging choice related to geographic separation of sub-populations.

Prey items found in stomachs of narwhals include Polar cod (*Boreogadus saida*), arctic cod (*Arctogadus glacialis*), *Gonatus* squid spp., shrimp (*Pandalus sp.*), and Greenland halibut. Narwhal prey selection and foraging intensity have a strong seasonal component (Finley and Gibb 1982, Chapter 4). In spring, narwhals take arctic or Polar cod at the sea ice edge. In summer, foraging intensity declines and food consumption is at a minimum, supported by hundreds of empty stomachs in harvested animals (Mansfield et al. 1975, Finley and Gibb 1982, Heide-Jørgensen et al. 1994, Chapter 4). Foraging intensity resumes in the fall as whales move south (Finley and Gibb 1982) and peaks during winter. The bulk of the energy gain appears to be taken on the wintering grounds, with the primary prey item being Greenland halibut. All stomachs examined during winter harvests in Disko Bay, West Greenland (n=20) were completely full and contained large amounts of fleshy undigested material, with >50% containing Greenland halibut as the only prey item (Chapter 4). The regularity of deep dives to ≥800 m during the five month period on the offshore wintering grounds together with the occurrence of full stomachs with fresh remains during coastal winter harvests are strongly consistent with offshore foraging activity on Greenland halibut (Chapter 3).

Greenland halibut are widely distributed in the Northwest Atlantic and are found in a continuum from Davis Strait northward into Baffin Bay. Their spawning area is believed to be located in Davis Strait, south of 64°N at depths >1,200 m. Larvae are carried north and young fish settle on the slopes southwest of Disko Island in water no deeper than 400 m. Young halibut then migrate to Baffin Bay or coastal deep-water fjords as they grow into adults (Riget and Boje 1989, Jørgensen 1997a). Greenland halibut in Davis Strait and Baffin Bay, most likely constituting a single stock (Treble and Jørgensen 2002), are an economically important resource in the Davis Strait and are the basis of one of the most important fisheries in Greenland (Jørgensen 1997b). Traditionally the fishery for Greenland halibut has taken place in the fjords of Northwest Greenland with longlines and gillnets (Riget and Boje 1989) with annual catches around 20,000 tons (Anon. 2002). In the 1990s an offshore fishery developed in Davis Strait with total catches around 10,000 tons annually (equal amounts taken in Canadian and Greenland waters). Within the past decade, exploitable offshore resources of Greenland halibut have been discovered in deeper, central Baffin Bay (Boje and Hareide 1993, Treble et al. 2000, Treble and Jørgensen 2002). Exploratory licences have been issued for an offshore fishery at depths between between 800 to 1,200 m resulting in catches between 300-2,600 tons annually (Treble and Bowering 2002).

In Baffin Bay and Davis Strait, Greenland halibut are assessed by the Northwest Atlantic Fisheries Organization (NAFO). The Total Allowable Catch (TAC) increased from 11,000 to 19,000 tons between 2000 and 2002 (Treble et al. 2000, Jørgensen 2002). Annual scientific surveys for Greenland halibut conducted between 1999-2001 in Baffin Bay and Davis Strait estimated about 300,000 tons of this species. The surveys mostly covered depths between 400 and 1,500 m, with highest densities found between 800 and 1,200 m in all three years (Treble et al. 2000, Treble et al. 2001, Treble and Jørgensen 2002, Jørgensen 2002).

Narwhals from West Greenland and the Canadian high Arctic have a sympatric distribution with the deep-water Greenland halibut resources in Baffin Bay (Dietz et al. 2001, Heide-Jørgensen et al. 2002a, Treble and Bowering 2002). Additionally, they show concentrated diving behaviour within the depth range of high Greenland halibut densities (Laidre et al. 2003). Because the entire population of narwhals from Canada and West Greenland winter in these restricted areas for over 50% of their annual cycle, the Greenland halibut population probably is subject to a large impact from narwhal predation.

A large sub-population of narwhals wintering in northern Baffin Bay exhibits more frequent and shallow dives during the winter period than a smaller sub-population of narwhals wintering in southern Baffin Bay (Laidre et al. 2003). This suggests the group in southern Baffin Bay targets prey on the bottom more frequently than narwhals farther north. Whales in the northern area are also located in much deeper water than the southern area and the bottom may not be easily reached. Consequently, larger impacts of narwhal predation on benthic Greenland halibut should be detected in the southern area. The objectives of this study were twofold: first, to examine if the populations of Greenland halibut in Baffin Bay could sufficiently support levels of narwhal predation estimated by a bioenergetic model; and second, to determine if the impacts of narwhal predation in focal areas could be detected based on data collected during bottom trawl surveys for Greenland halibut between 1999-2001.

METHODS

Bioenergetic model

A stage and mass structured population model was developed using proportional stage classes reported by Koski and Davis (1994), where age classes of narwhals were obtained based on size and color of individuals (n=1,230) observed during aerial surveys in Baffin Bay. Relative proportions were calculated for three stage classes: juveniles (14% of the population), immatures (19%), and adults (67%). Sex ratios were assumed to be 50% juvenile and immature females and 55% adult females based on Koski and Davis (1994). Stage-specific body masses were calculated from physical data from 38 whales taken by Inuit hunters in Uummannaq, West Greenland, in 1993. Body mass for immature and mature narwhals was distinguished based on the size of sex organs. The median body mass for sexually mature males (1,350 kg) was obtained by regressing mean testis weight against body weight (n=29). The median body mass for sexually mature females (925 kg) was obtained by regressing mean uterus weight and number of corpora marks against body mass (n=9) (Heide-Jørgensen, unpublished data). The median body mass for juveniles was 175 kg, and the median body mass for male and female immatures was 600 kg and 475 kg, respectively.

A generalized bioenergetic model was developed to quantify the daily energetic needs for each stage and sex class of discrete sub-populations of narwhals wintering in Baffin Bay. The model was used to estimate gross daily energy requirements (kcal/d) by extrapolating individual estimates to population abundance estimates (Heide-Jørgensen et al. 2002a, Innes et al. 2002). Basal metabolic rate was calculated and additional energy required for activity, growth, and reproduction was added into the model as proportions of basal metabolic rate. The simple bioenergetic model framework was:

$$ER = \frac{[BMR(A+G+R)]}{DE * AE}$$

where *ER* =energy requirement in kcal/day for an individual, *BMR*=basal metabolic rate (kcal/day) calculated as:

$$BMR = 70 * W^{0.75}$$

where W = the body mass in kg (Kleiber 1975). *A* is an activity metabolic multiplier, *G* is a growth multiplier, *R* is the reproduction costs multiplier for adult females (costs of fetal metabolism, fetal growth, and lactation), *DE* is the digestive efficiency (digestible energy), and *AE* is the assimilation efficiency (digestibility of dry matter).

The factor (*A*) used to account for activity metabolism essentially assumes that active metabolism is a constant multiple of basal metabolic rate, an approach used in several recent bioenergetic models for marine mammals (Lavigne 1995, Kenney et al. 1997, Winship et al. 2002). Active metabolism can be attributed to foraging behavior, movement or migration, or age or sex-specific behavior, and has been estimated to be 2 to 5 times BMR in cetaceans (Lockyer 1981, Folkow and Blix 1992, Kenney et al. 1997). A mean value of 2.5 was used following Hooker et al. (2002) and Kenney et al. (1997).

Juveniles have additional energy requirements specifically for growth, which decrease with increasing age until physical maturity. These requirements can be 110-300% of the maintenance energy required for adults (Innes et al. 1987, Murie and Lavigne 1991, Hammill et al. 1997, Winship et al. 2002). Therefore, growth in body mass or production was modeled as additional needs (varying with age) and calculated as a proportion of BMR. We assumed a standard *G* (growth multiplier) of 2.0 for juveniles, and let *G* range from 1.0 to 2.0 for the immature stage classes. *G* was not applied to the adult stage classes assuming physical maturity was reached and there were no further growth requirements.

Energy for reproduction (*R*) for adult females was estimated for the costs of pregnancy and the costs of lactation. Narwhals were assumed to have a calf every three years (Hay 1984), and consequently, within a given year a mature adult female was either pregnant, lactating, or resting. A composite energy requirement for pregnancy was based on the following: the fetus (mean mass = 50 kg, Hay 1984) was assumed to have a BMR proportional to that of an adult per kg (Yasui and Gaskin 1986) and the cost of fetal growth (450 day gestation period) was calculated using Brody's (1945) equation for the heat increment of gestation, Q, where $Q = 4400 M^{1.2}$, where M is the mean birth mass (100 kg). Therefore, $R_{(pregnancy)}$ was estimated as combined costs of energy for fetal metabolism + energy for fetal growth.

The cost of lactation in free-ranging cetaceans has not been studied to the same extent as pinnipeds but is assumed to be three times the combined cost of fetal growth and basal metabolism based on values reported for captive harbor porpoise (*Phocoena phocoena*) (Yasui and Gaskin 1986). The cost of lactation was approximately twice the basal metabolic rate (2*BMR), which corresponds well with that reported for captive belugas (*Delphinapterus leucas*) and Atlantic bottlenose dolphins (*Tursiops truncatus*) (Kastelein et al. 1994, Kastelein et al. 2002). This rate was also in good agreement with that found for otariids (Winship et al. 2002). The costs of pregnancy and lactation were combined to create a value for *R* of 0.78 for the adult female portion of the population.

Digestive and assimilation efficiencies (*DE* and *AE*) were adopted from the literature following that found for marine mammals that forage on fish (Härkonen and Heide-Jørgensen 1991, Hammill et al. 1997, Lawson et al. 1997a, Lawson et al. 1997b, Croll and Tershy 1998, Winship et al. 2002). Estimates of AE and DE for cetaceans that prey on Greenland halibut do not exist. Therefore, estimates were taken from captive harp seals (*Phoca groenlandica*) fed Greenland halibut with a *DE* of 0.95 and an *AE* of 0.89 (Lawson et al. 1997a). The energetic value of Greenland halibut was assumed to be 5.5 kJ/g (Lawson et al. 1998). Finley and Gibb

(1982) reported information on the size classes of Greenland halibut taken by narwhals, which ranged from 45-60 cm, with the largest whole specimen measuring 61 cm and a mass of 2.4 kg. Based on catch data from 1995-2001, Greenland halibut in the 45-60 cm size class correspond to masses of 0.7-2.3 kg (ages 6-10 years) (Jørgensen 2002). We used an approximate median length (52 cm) corresponding to a mass of 1.2 kg in the model.

Error in parameter estimation was addressed with Monte Carlo simulations, where parameter values were randomly selected from sampling distributions that best described their uncertainty (Manly 2002). Activity and growth multipliers were sampled from a uniform distribution, where A varied between 2 and 3 for all stage classes and G varied between 1 and 2 for immatures and juveniles. Population size was drawn from a lognormal distribution, both for the northern wintering ground (Innes et al. 2002) and the southern wintering ground (Heide-Jørgensen et al. 2002a). Approximately 10,000 simulations were used to calculate a mean caloric requirement and 95% CI for the winter period. The biomass of Greenland halibut required to fulfill the energetic needs on the two wintering grounds was estimated with the proportion of Greenland halibut in the diet varying between 25-75%.

Narwhal satellite data

The spatial and temporal distribution of narwhals in Baffin Bay was determined from data from satellite tracking of narwhals between 1993 and 2001. Because narwhals are forced out of high Arctic areas by October due to forming fast ice, 100% of each sub-population was assumed to occupy Baffin Bay for 5 months (150 days) of the year. The temporal period of residence was based on results from two satellite tagged female narwhals tracked for 14 months documenting timing of arrival (November) and departure (April) from the wintering grounds (Heide-Jørgensen et al. 2003a). All spatial analyses were conducted in the Geographic Information System ESRI ArcGIS 8.3.

To date, three sub populations of narwhals have been satellite tracked into two wintering grounds in Baffin Bay (Figure 5.1). The 95% kernel probability area estimates, derived from the satellite tracking geographic data, were used to identify wintering regions occupied by sub-populations that have been surveyed for abundance (Heide-Jørgensen et al. 2002a, Heide-Jørgensen et al. 2003a, Figure 5.1). This method was chosen because it was possible to confine a known number of whales (with associated variance estimates) into an explicit spatial region and draw conclusions on predation impacts by linking narwhal area use, distribution, and abundance.

The northern wintering ground, in central Baffin Bay, approximately 25,486 km^2, is used by the sub-population of narwhals from Somerset Island, Canada. Recent line-transect surveys accounting for observer and availability bias in the summer range in 1996 estimated an abundance of 45,358 whales (CV 0.35) in this region (Innes et al. 2002). The southern wintering ground, approximately 10,671km^2, is occupied by two narwhal sub-populations from Melville Bay, West Greenland and Eclipse Sound, Canada, numbering 5,348 (CV 0.43) based on line transect surveys on the wintering grounds in 2000 corrected for availability and perception bias (Heide-Jørgensen et al. 2002a). Only the surveyed portion of the southern region was used in the model. The north and south wintering regions are spatially distinct and no overlap or exchange has been observed based on satellite tracking studies (Dietz et al. 2001, Heide-Jørgensen et al. 2002a, Heide-Jørgensen et al. 2003a). The caloric requirements for whales occupying the two separate wintering areas were estimated with the bioenergetic model.

Data on fish abundance, density and length frequencies

Data on abundance, biomass, and length structure collected during scientific surveys targeting Greenland halibut in 2001 were used to examine spatial differences in Greenland halibut catches or other potential narwhal prey catches inside and outside narwhal wintering grounds. Surveys were conducted between 16 September and 15 November aboard the research vessel *Paamiut* using an Alfredo III bottom trawl with rock hopper gear. Mesh size was 140 mm with a 30 mm liner in the codend. Average towing speed was 3.0 kn. Towing time was approximately 30 minutes and tows as short as 15 minutes were included in the analysis. Trawling took place during both day and night and surveys were conducted down to 1,500 m on either side of Baffin Bay and in Davis Strait (Figure 5.1). The survey was directed towards Greenland halibut, however, information on all other fish species collected in each tow was also recorded.

Numbers and total mass were recorded on a tow-by-tow basis for each species and individual lengths were measured for most species. All catches and length frequencies were standardized to square kilometer swept (for additional information on methods see Jørgensen 1998). Trawl data in Baffin Bay were examined for latitudinal or longitudinal trends in density by pooling tows into 2-degree latitude intervals and classified as falling on the west or east side of the Baffin Bay midline. All years where sampling occurred on one or both sides of Baffin Bay were examined. ANOVAs were conducted to examine latitudinal trends at each 2-degree interval and t-tests were conducted to examine longitudinal trends on either side of Baffin Bay.

Each tow was assigned to one of five areas: within the northern wintering ground range (NWG), the southern wintering ground range (SWG), Baffin Bay (BB) defined as all tows in west Baffin Bay which were north of 67.5°N, North Davis Strait (NDS) defined as all tows between 67.5°N and 65°N, and South Davis Strait (SDS) defined as all tows south of 65°N (Figure 5.1). Tows were considered to be in a whale wintering ground if they were within or bordering the home range polygon. Tows that fell between the two wintering areas on the east side of Baffin Bay were not used in the analysis because some of the regions are used by other aggregations of wintering narwhals.

Greenland halibut densities and length composition are influenced by depth (Jørgensen 1997a) and analysis of densities and length composition of Greenland halibut were hence restricted to survey tows taken at depths ≥800 m. This depth was selected based on narwhal dive behavior studies that indicated aside from near surface dives (0-50 m), the largest proportion of diving on the SWG occurs in depth categories ≥800 m (Laidre et al. 2003). These depths coincided with depths where Greenland halibut were most abundant.

Mean densities expressed as kg/km^2 or the number of fish/km^2 in all length classes grouped into 3 cm intervals, were calculated for each of the five regions for both Greenland halibut. Mean fish densities and biomass were also calculated for other potential narwhal prey species including Roughead grenadier *(Macrourus berglax)*, Deep-Sea Redfish (*Sebastes mentella*), Threadfin rockling (*Gaidropsaurus ensis)*, and especially in the Baffin Bay area, Snailfish (*Liparis fabricii),* Arctic skate (*Raja hyperborea)* and Polar cod (Treble et al. 2000, Treble 2002, Jørgensen 2002). Mean densities between regions were compared using ANOVAs and Tukey's HSD post hoc analyses. The distribution of the standardized length frequency (number/km^2 and percent/km^2) of Greenland halibut in each region was compared statistically with the two sample Kolmogorov-Smirnov test. Differences in biomass due to region-based densities for Greenland halibut and other fish species were examined and compared to the results of the bioenergetic model for areas with varying levels of predation.

RESULTS

Bioenergetic predictions on the Northern Wintering Ground

Predicted relative daily food requirements were highest for young animals (6% and 5% of body mass for immature males and females, respectively) and lowest for adults (3-4% of body mass). The bioenergetic model produced a daily sub-population energy requirement for the

NWG (45,000 whales) of 19×10^8 kcal/d (SD 7.1×10^8) (Table 5.1). The adult female portion of the population had the highest energy requirements, 8.1×10^8 kcal/d (SD 3.0×10^8) with adult male stage class following them at 6.7×10^8 kcal/d (SD 2.5×10^8 kcal/d). If the daily energetic needs of the sub-population were met with a diet that was comprised of 50% Greenland halibut, the sub-population would require 738 (SD 272) metric tons of Greenland halibut per day. The estimated biomass of Greenland halibut required by the NWG whales for the 5 month winter period ranged from 55,360 (SD 20,377) to 166,081 metric tons (SD 61,130) (Table 5.1). Nearly all the variation in the model was a result of uncertainty in population size.

Bioenergetic predictions on the Southern Wintering Ground

Model simulations for the sub-populations occupying the SWG (5,000 whales) resulted in a population caloric requirement of 2.4×10^8 kcal/d (SD 1.1x $\times 10^8$) (Table 5.2). If the daily energetic needs of the sub-population were met with a diet that was comprised of 50% Greenland halibut, the sub-population would require 90 metric tons (SD 40) of Greenland halibut per day. The estimated biomass of Greenland halibut required by the whales on the SWG for the 5-month winter period ranged from 6,768 (SD 3,004) to 20,304 (SD 9,014) metric tons (Table 5.1).

Greenland halibut densities

No effects of latitude on Greenland halibut density could be detected for the west side of Baffin Bay in 1999 ($p=0.29$), the west side of Baffin Bay in 2001 ($p=0.57$), or the east side of Baffin Bay in 2001 ($p=0.86$) (the east side of Baffin Bay was not surveyed in 1999). East-west comparisons of Greenland halibut density at the same 2-degree latitude intervals in 2001 indicated significant differences only for tows between 66-68°N ($p<0.05$). This was the latitude range of the SWG (on the east side of Baffin Bay), and densities were higher on the west side. No other longitudinal comparisons produced significant differences.

During the 2001 Greenland halibut survey 205 tows were made at depths varying from 145 m to 1458 m. Of those, 106 tows were $\geq$800 m; 13 were in the NWG, 9 were in the SWG, 15 were in West Baffin Bay, 7 were in North Davis Strait, 51 were in South Davis Strait, and 11 tows were outside the NWG on the eastern side of Baffin Bay and excluded from this analysis. Greenland halibut were caught on 201 tows and length classes ranged from 10 cm to 110 cm (Table 5.2).

The lowest density of Greenland halibut (kg/km^2) was found in the SWG, which was about half of all other regions (Table 5.2). The highest densities were found in the regions without narwhals (Baffin Bay and South Davis Strait). There were significant differences between densities in the five regions ($p<0.01$) and post hoc analyses indicated differences occurred between the SWG and both Baffin Bay and South Davis Strait ($p=0.01$). Mean densities on the NWG were not different from the SWG or any other areas.

Length distribution of Greenland halibut

The number of fish per square kilometer (Figure 5.3) was examined in 3 cm incremental length categories with Kolmogorov-Smirnov tests. Significant differences were found between the SWG and Baffin Bay ($p=0.002$), the SWG and North Davis Strait ($p=0.016$), and the SWG and South Davis Strait ($p=0.033$). The northern wintering ground was also significantly different from Baffin Bay ($p=0.021$), however, the NWG was not significantly different from the SWG. When the length frequency distributions were compared visually, the length frequencies in the SWG (and to some extent also the NWG) were relatively flat compared to other areas (Figure 5.3). The statistical difference was due to fish in the ranges of 35-55 cm missing from the two whale wintering grounds.

Greenland halibut biomass differences

The results of the bioenergetic model were related to the observed differences in Greenland halibut density between areas with predicted high (SWG), low (NWG), and no predation (Baffin Bay and Davis Strait) by calculating the biomass differences between regions. Greenland halibut biomass on the SWG was estimated at 7,124 metric tons using a mean density of 667 kg/km^2 (Table 5.2). The biomass estimate for an area of comparable size in Baffin Bay was estimated as 25,775 metric tons using a mean density of 2,416 kg/km^2 (Table 5.2). The difference between the densities in these two areas was approximately 18,651 tons fewer fish in the SWG. This value fell within the 95% confidence intervals for a diet of 50% Greenland halibut (mean of 13,536 metric tons removed) or 75% Greenland halibut (mean of 20,304 metric tons removed) from the bioenergetic model developed for the sub-population occupying the SWG (Table 5.1). When the same analysis was conducted comparing the SWG densities to South Davis Strait (mean density of 2,184 kg/km^2), a difference of 16,182 tons was achieved.

Although the density on the NWG was not significantly different from other study areas, it was still much lower than that in the western part of Baffin Bay. Using the NWG mean density of 1,295 kg/km^2, the biomass of Greenland halibut on the wintering ground was approximately 33,479 metric tons. When the biomass differences between the NWG and Baffin Bay were examined across an area comparable to the NWG (25,846 km^2) (Table 5.2), a difference of 28,950 metric tons was produced. The results of the bioenergetic model indicated that this sub-population would consume somewhere between 55,360-166,081 metric tons of Greenland halibut (Table 5.1) over 5 months (25-75% diet), exceeding estimates of total Greenland halibut biomass in the region.

Other species densities and abundance

The mean densities of pooled 'other fish species' collected during the bottom trawls were examined for each of the five regions (Table 5.2). Relative to densities found for Greenland halibut, densities of other fish species in all regions were substantially lower (45-97% less), with no single region higher than 450 kg/km^2. The pattern of densities was also different. The highest densities of other species were found in the SWG and South Davis Strait. Densities were lower in Baffin Bay, the NWG, and North Davis Strait.

The densities of the other bottom trawl fish species were used to estimate biomass in the different regions. Approximately 4,000 tons of other fish species exist in the SWG or South Davis Strait, with other regions such as Baffin Bay and the NWG as low as 700-1,400 tons. Making the conservative assumptions that the other pooled fish species had approximately the same energetic value as Greenland halibut, the entire biomass of other species would support, at most, 25% of the SWG sub-population needs, and no more than 7% of the NWG sub-population needs.

The abundance of Polar cod was examined separately from other fish species. The abundance of Polar cod significantly increased with increasing latitude both on the west and east side of Baffin Bay. When the abundance was examined by 1-degree increments of latitude, estimates increased linearly from 66-73°N, ranging from 15 fish/km^2 (SD 35) to 6,555 fish/km^2 (SD 9,987). Large catches did not occur below 70°N and the mean abundance increased by a factor of 5-15 at latitudes above 71°N. The length of Polar cod ranged from 4-24 cm. The large number of zero observations for Polar cod was likely due to the species tendency towards schooling behavior. Furthermore, Polar cod is pelagic and abundance estimates from the Greenland halibut survey can only be considered indicative.

DISCUSSION

Bioenergetic model

An energy budget model is never assumption free, and in the case of missing data or unknowns for a species, values must be adopted (and scaled appropriately) from other sources. There have been many attempts to quantify the energetic requirements and total food consumption of various marine mammal populations (Yasui and Gaskin 1986, Härkonen and Heide-Jørgensen 1991, Murie and Lavigne 1991, Kastelein et al. 1993, Lavigne 1995, Hooker et al. 2002, Winship et al. 2002). These models are clearly generalizations and rely on basic physiological parameters, energy required for different life stages, and diet assumptions. Life history characteristics and detailed age-structured population models for narwhals are hindered by the lack of a reliable method for determining exact age of individuals. Consequently, only information on proportions of individuals in different stage classes is available from coastal observations during the summer period or summer harvest data.

We have made a number of simplifying assumptions about energetic requirements of narwhals in Baffin Bay. The high degree of uncertainty introduced by scaling energy use from the level of the individual to the level of the population is additive across all input variables and multiplicative across population size and time, and inclusion of great detail may result in a loss of precision (Boyd 2002, Mohn and Bowen 1996). Although comprehensive detailed models have been built attempting to incorporate this uncertainty (Boyd 2002), here we present a minimum realistic model. The results of individual energy requirements in this analysis compare well with that reported in Welch et al. (1993), who estimated an 880 kg beluga would require approximately 22 kg of cod per day. In this study, an adult female narwhal (925 kg), a close Arctic relative of the beluga, required approximately 4.5×10^4 kcal/d, resulting in a maximum of 35 kg of Greenland halibut. Energy requirements also follow well with that reported for captive belugas (Kastelein et al. 1994).

Greenland halibut predation

Large and significant differences in Greenland halibut density were observed between the SWG and other areas (Table 5.2, Figure 5.1). The lowest Greenland halibut density occurred in the SWG, which was the region with the hypothesized highest predation rates. The only other survey year that allowed for comparison to the 2001 values was that from 1999. The overall mean Greenland halibut density from 24 tows $\geq$800 m taken during the 1999 survey in Baffin Bay was 2,037 kg/km^2 (SE 365), quite similar to that observed in the same area in 2001 (mean 2,416 kg/km^2, SE 589) (Table 5.2). The survey in 1999 did not cover the core area of the SWG and tows were only taken on the periphery or outside of the range. The density from tows (n=10) close to the SWG was indeed lower than Baffin Bay (1,161 kg/km^2), however, not to the degree that was found for 2001 data. The single tow that was taken directly inside the core SWG range had a density of 285 kg/km^2, comparable to the lower densities observed in 2001.

The bioenergetic model results for narwhals on the SWG compared exceptionally well with the observed differences in Greenland halibut density between the SWG and Baffin Bay and South Davis Strait. Of course, these estimates are not exact and contain error introduced both by the bioenergetic model and the Greenland halibut trawls. However, the results were within the same order of magnitude of difference estimated by applying observed Greenland halibut densities from the different areas to a region comparable to the size of the SWG. These results also fell within 95% confidence intervals reported for a diet of 50% and 75% Greenland halibut.

On the NWG, the bioenergetic model and observed Greenland halibut densities indicated that Greenland halibut cannot, and most likely do not, play the same role in the diet of the narwhal they do on the SWG. The estimate of a diet of 25% Greenland halibut consumption on the NWG resulted in a consumption estimate that was higher than the estimated biomass of Greenland halibut in the NWG. Although the biomass estimates of Greenland halibut can only be considered index values, results indicate that the NWG sub-population must rely less on Greenland halibut and utilize alternative food sources. This agrees with observations of increased number of dives and time spent at mid-water. Note that the density of Greenland halibut in the NWG was still lower than in Baffin Bay, suggesting some predation may occur but not to the extent observed on the SWG.

The differences in length frequency distributions between whale wintering grounds and non-whale areas may be indicative of selective removal of specific size classes of Greenland halibut. There appears to be a relative lack of Greenland halibut in the 35-55 cm range in our data, which matches well with the most common size classes taken by narwhals, 45-60 cm, reported by Finley and Gibb (1982). Chapter 4 reported narwhals in Disko Bay, West Greenland took Greenland halibut ranging from 9 to 55 cm, with a mean of 36 cm (SD 9). The length frequency difference was most pronounced on the SWG, and less so on the NWG. In Davis Strait, it has been demonstrated that Greenland halibut gradually move towards the presumed spawning area in the Davis Strait as they grow (Jørgensen 1997a). To what extent such a migration takes place in the Baffin Bay is not known, as the observations from Davis Strait were based on relatively small changes in length frequencies and increases in mean size by latitude. Fishing influences are low and both narwhal wintering grounds have been essentially unfished with only slight pressure on the SWG in recent years (less than 300 tons for 1996-2000). Only because of the pristine nature of the study area is it possible to link the low numbers and skewed length frequencies of Greenland halibut in restricted areas to predation by narwhals.

Densities and biomass of Greenland halibut in this study were not adjusted for trawl gear efficiency, however this bias was not expected to be significant. The gear used in this study was ideal for halibut 10-50 cm in length (within the range targeted by narwhals) and any negative bias was more specifically directed towards fish larger then 50 cm or fish in the first two year classes (<17 cm). The same ship and gear was used throughout the surveys on all tows in all years. Despite an overall negative bias when estimating total densities or biomass of fish in an area from trawl data (present in all trawl surveys), gear efficiency was likely a small contribution to the differences found in Greenland halibut densities between areas.

Accounting for differences in production between regions is complicated in any fisheries model, especially when only sparse information exists. Differences in production between the wintering grounds and other areas of Baffin Bay were expected to be minimal in this study. This is primarily due to the fact that Greenland halibut are recruited from the spawning ground in Davis Strait and are carried north by currents. Fish that end up on the slopes of Baffin Bay, where narwhals feed for six months, are lost to the dynamics of the population because they do not move south again to spawn. Furthermore, the epicenter of dispersal recruitment for Greenland halibut is located very close to the SWG, the area where the lowest densities of halibut were found.

Polar cod, squid, and other species

The pattern of increasing abundance of pelagic Polar cod with increasing latitude may offer insight into the observed diving behavior on the NWG (Figure 5.2). Schools of pelagic Polar cod may be an alternative food source in the deep, potentially unexploitable habitat of the NWG, where reaching the bottom for Greenland halibut regularly might be costly. Assuming travel of 2 m/s, it would take a narwhal >30 minutes round trip to travel to 2,000 m, essentially eliminating any foraging time given aerobic dive limits (Laidre et al. 2002). The relative lack of Polar cod on the lower latitude SWG, together with the combination of reachable benthic depths, may functionally focus foraging behavior on Greenland halibut. Note that the density of whales on the NWG is four times the density on the SWG. It may be necessary for a larger concentration of whales to exploit several food sources to meet collective food requirements. The substantial increase in the abundance of Polar cod above 71°N (the NWG is located between 71-72.5° N) may provide this alternative (Figure 5.2).

The pattern of declining Greenland halibut densities with increasing hypothesized predation levels was not observed for densities of the other potential prey. It is interesting to note the SWG had one of the highest densities of other fish species (together with South Davis Strait) of the five regions and the results indicate that densities obtained for Greenland halibut in the SWG are not merely a reflection of overall low productivity. The biomass of other fish species on the wintering grounds does not appear to be high enough to support the predation levels estimated by the bioenergetic model for either wintering ground. Therefore, either a significant portion of the predation on and close to the seafloor must come from the Greenland halibut population, or whales must also exploit more abundant mid-water prey species not examined here.

A large portion of the diet of other deep diving odontocetes in the North Atlantic, the bottlenose whale (*Hyperoodon ampullatus*), pilot whale (*Globicephala melaena*), and sperm whale (*Physeter macrocephalus*), is post-juvenile *Gonatus* squid species (Desportes and Mouritsen 1994, Hooker et al. 2001, Santos et al. 1999, Santos et al. 2001). Juvenile *Gonatus* occupy surface waters and gradually move to deeper depths as they age. Adults are common both on the bottom and at mid-water depths on the continental slopes (post-juvenile squid have been caught at depths of 200-600 m) (Kristensen 1984, Santos et al. 2001a). Estimates of density, vertical and horizontal distribution of post-juveniles in West Greenland and Baffin Bay are relatively unknown (Piatkowski and Wieland 1993). Surveys conducted for *Gonatus* in Baffin Bay only report density estimates of larvae at the surface or depths of juveniles between 70-80 m (Kristensen 1984, Piatkowski and Weiland 1993).

Gonatus squid remains have been found in all seasons in narwhal stomachs and approximately 35% of winter stomachs were dominated by fresh *Gonatus fabricci* remains (Chapter 4). Little is known about the density or spatial distribution of *Gonatus* in Baffin Bay. Squid were observed frequently down to depths of 1,400 m in this study, but the representative catch from a bottom trawl towed at 3 knots is poor and is not useful for estimating squid abundance with any reliability. Hobson et al. (2002) report the narwhal diet contains some proportion of non-fish species, probably squid and shrimp, based on stable isotope analyses. As there appears to be some amount of sub-population specific-foraging behavior, sub-populations of narwhals, including those on the NWG, may utilize *Gonatus* to a larger degree than those found farther south.

Baffin Bay and Davis Strait

The bioenergetic estimates for the NWG were derived from an abundance estimate of 45,358 (CV 0.35) narwhals where only a portion of the narwhal summer range was surveyed (Innes et al. 2002). An additional 5,000 narwhals, based on the estimate in Heide-Jørgensen et al. (2002) for whales summering in Eclipse Sound and Melville Bay, indicate there could be at least 50,000 narwhals in Baffin Bay. Whales from other summering sub-populations such as Admiralty Inlet, Canada or Inglefield Bredning, Greenland, and wintering aggregations off of Disko Island, Greenland have not been included in these estimates and may add up to 10,000 more whales. Koski and Davis (1994) produced an uncorrected estimate of 34,363 narwhals (SE 8,282) wintering in Baffin Bay based on line transect surveys conducted in late spring 1979. This estimate supports the view that narwhals undoubtedly occur in large numbers and are major predators in the Baffin Bay ecosystem.

Foraging on the wintering ground

There is strong evidence that foraging intensity peaks during winter and that a large proportion of the annual energy is consumed in Baffin Bay (Chapter 5). Narwhals have limited options for making long-distance movements to search for schools of squid or other pelagic fish. They are confined to regions with open leads and cracks, as they are not able to break through the pack ice to create breathing holes. Long distance, horizontal foraging trips at mid-water depths would be risky due to a potential need for air in a region without leads. A relatively sedate, bottom-dwelling prey such as the Greenland halibut would provide a more stable source of food for the whales during the 5-month period they are in the ice, as foraging intensity could be focused in the vertical plane with fewer risks. If whales occupy depths at which the bottom cannot be efficiently reached regularly, then the winter regions must contain a reliable mid-water food source, which is spatially distributed such that it can be exploited without risk of ice entrapment or closure.

Concentration of prey is an important factor influencing choice and probability of capture. Patchy prey availability in the marine environment will affect foraging behavior, residence times, and prey choice. When an individual or group of consumers locates high concentrations of a rich and profitable food source, it may be worth concentrating their foraging energy and foraging time to maximize their gain from the patch, regardless of the energetic tradeoff. Top marine predators are inclined to be aggregated in focal areas or tend to be central place foragers. Consequently changes in local prey abundance or density may have a larger effect on foraging than changes in prey across a large range. Suitable prey aggregations providing the critical density thresholds necessary for intense winter-feeding of narwhals may be impacted by increased offshore fishing activities. Based on evidence of minimal feeding on the summering grounds and intense feeding on the wintering grounds, narwhals appear to maximize energy gain and fat storage in areas with reliable prey in Baffin Bay. Consequently, this choice reinforces the importance of the wintering grounds to narwhal sub-populations in Canada and Greenland, and indicates that the future increase in fishing operations in deep-waters of Baffin Bay in the primary wintering areas may affect food availability or foraging success for some sub-populations.

Table 5.1. Bioenergetic requirements for two narwhal sub-populations occupying wintering grounds in Baffin Bay (daily needs are extrapolated to 5 month period) with predicted removal of Greenland halibut (in metric tons). The biomass removal was calculated by varying the percentage of Greenland halibut in the narwhal diet between 25-75%.

Area	Mean energy requirement (kcal/5 mos with SD)	25% Greenland halibut diet		50% Greenland halibut diet		75% Greenland halibut diet	
		Mean	95% CI	Mean	95% CI	Mean	95% CI
NWG	2.9×10^{11} (1.1×10^{11})	55,360	26,531-105,179	110,720	53,063-210,359	166,081	79,594-315,538
SWG	3.6×10^{10} (1.6×10^{10})	6,768	2,675-14,163	13,536	5,351-28,326	20,304	8,206-42,489

Table 5.2. Summary information on survey tows for Greenland halibut (GHL) and other fish species in Baffin Bay and Davis Strait in 2001. Eleven tows were outside of the narwhals wintering grounds in the eastern side of Baffin Bay and were excluded from the analysis.

Region	n of tows	Number of GHL measured	Range of length categories for GHL (cm)	Mean density of GHL in kg/km^2 (SE)	Mean density of other fish in kg/km^2 (SE)
NWG	13	1,739	13-85	1,295 (185)	108 (21)
SWG	9	616	20-99	667 (325)	371 (151)
Baffin Bay	15	3,912	25-70	2,416 (589)	130 (29)
N. Davis Strait	7	1,255	18-104	1,762 (410)	66 (12)
S. Davis Strait	51	8,486	19-105	2,184 (156)	436 (32)
TOTAL	95	16,008	13-105	1,664 (314)	222 (75)

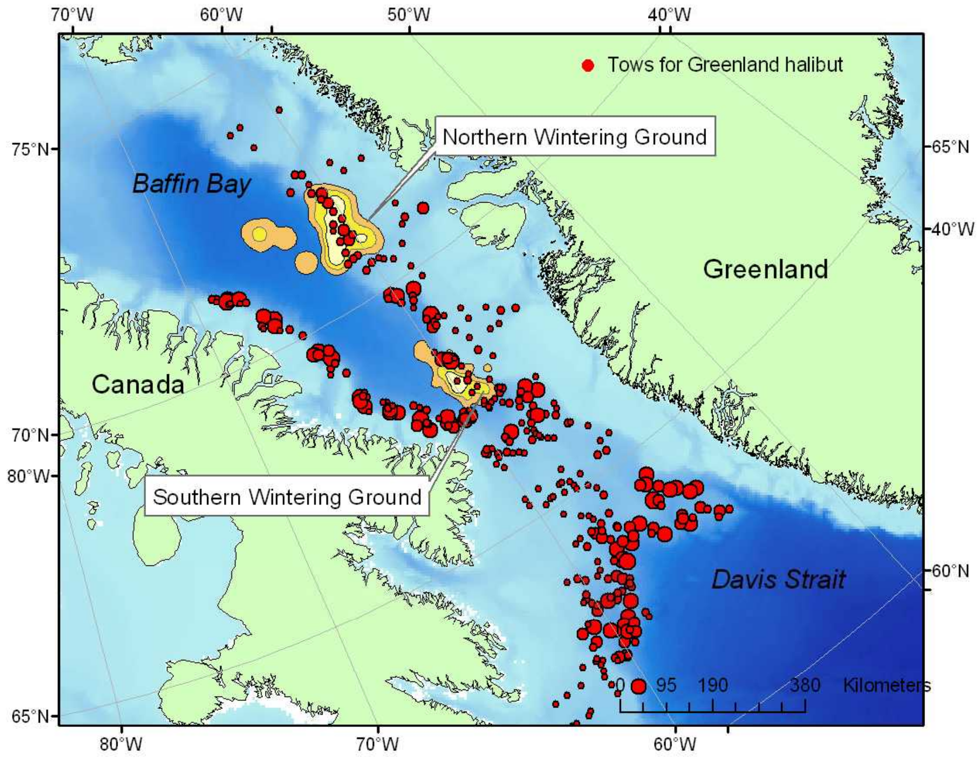


Figure 5.1. Map of study area, including northern and southern narwhal wintering grounds (NWG/SWG), and locations of trawl tows from the 2001 cruise used in the analysis. The relative proportion of area within the NWG (total 25,846 km^2) between 1,000 and 2,000 m was 15,679 km^2 and 7,573 km^2 greater than 2,000 m depths. The relative proportion of area within the SWG (total 10,674 km^2) was 9,130 km^2 between 1,000 and 1,800 m. There was no portion of the SWG beyond the 2,000 m depth contour.

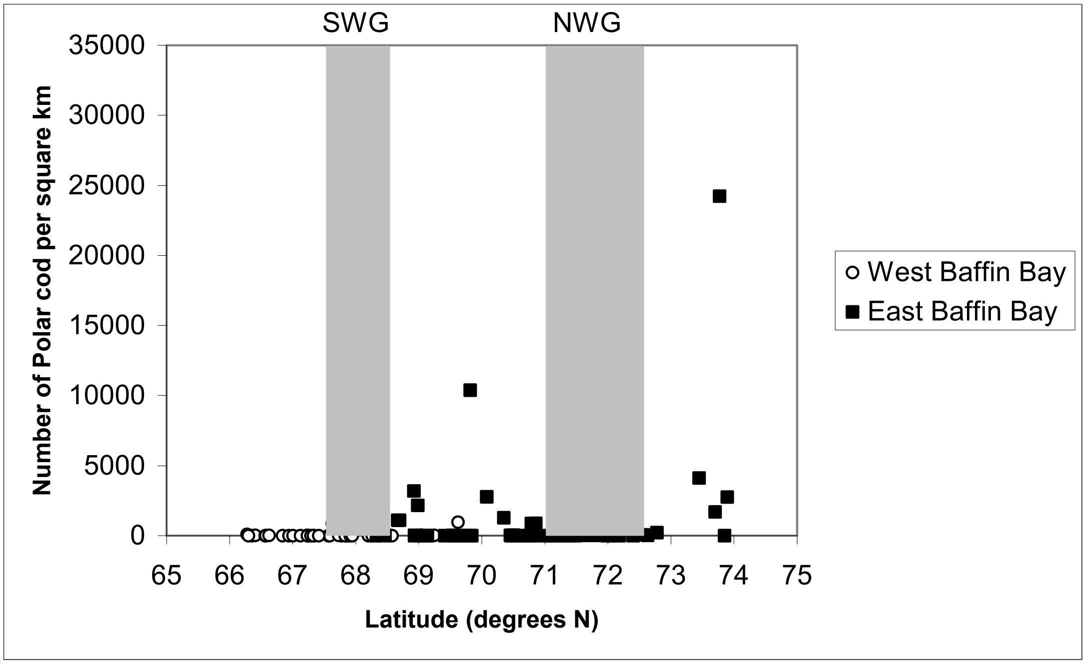


Figure 5.2. Abundance of Polar cod in West and East Baffin Bay, 2001, shown with latitude (degrees N) of each trawl location. The NWG and SWG latitude limits are shown as shaded. The large number of zero observations is due to the schooling behavior of the pelagic species.

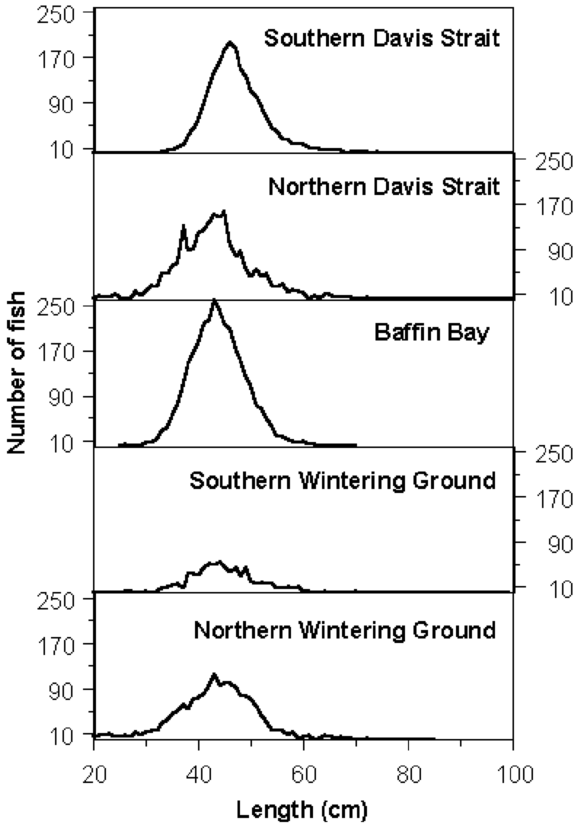


Figure 5.3. Distribution of the number of Greenland halibut/km^2 by length class in the 5 regions. The Southern wintering ground is hypothesized to have high predation levels, Northern wintering ground is hypothesized to have low predation levels, and Northern Davis Strait, South Davis Strait, and Baffin Bay are hypothesized to have little or no predation.

CHAPTER 6

FRACTAL ANALYSIS OF NARWHAL SPACE USE PATTERNS

INTRODUCTION

In predictably changing habitats, animals often alternate space use patterns in a predictable way. For habitat changes on a seasonal scale, responses often include switching between localized resource utilization and large-scale movements driven by migration. Behavioral changes resulting in differential movement patterns have been suggested as an effort to control environmental heterogeneity and create more stable life history responses to external perturbations (Ferguson et al. 1998a).

The narwhal (*Monodon monoceros*) is a high Arctic cetacean species whose annual movement patterns are strongly influenced by predictable seasonal changes in their environment. Narwhals have high site fidelity to summering and wintering grounds, yet their movements are also influenced by the spatial pattern of sea ice acting as a structuring agent. Narwhals spend the summer in the sheltered bays and fjords of the Canadian Arctic archipelago and West Greenland during the ice-free seasons. They migrate south in the fall before sea ice forms and spend the winter in Baffin Bay and North Davis Strait in restricted areas covered by dense offshore pack ice. In spring, they return to summering grounds following the receding sea ice edge. The annual round trip distance of the migration is up to three thousand kilometres (Heide-Jørgensen et al. 2002a). Detailed seasonal movement patterns of narwhals have been described for three separate sub-populations thought to be isolated based on satellite tracking and genetic studies (Dietz and Heide-Jørgensen 1995, Dietz et al. 2001, Heide-Jørgensen et al. 2002a). These sub-populations occupy two different wintering grounds in the Baffin Bay-Davis Strait area (Heide-Jørgensen et al. 2002a, Heide-Jørgensen et al. 2003a), where they show population-specific dive behavior and foraging preference (Laidre et al. 2003).

There is a high degree of spatial and temporal variability in Arctic marine habitats. Changes in climate, coupled with extreme seasonality in sea ice, influence primary and secondary production processes and ultimately the distribution and abundance of top predators (Ferguson and Messier 1996, Parkinson 2000a, Parkinson 2000b, Mauritzen et al. 2001, Root et al. 2003). In the case of Arctic cetaceans, the long-term effects of this variation are unknown both on local and global scales (Tynan and DeMaster 1997). A first step in understanding this link lies in quantitatively describing cetacean behavioural patterns and relating them to environmental heterogeneity in the context of seasonal changes.

A relatively new approach for assessing animal movement involves calculating the fractal dimension of paths, which describe variation in animal movement at a range of spatial scales across time (Mandelbrot 1983, Milne 1991, Turchin 1998). Fractals have linked to animal movement and terrestrial landscape structure for a wide range of species, from invertebrates (Crist et al. 1992, With 1994, Wiens et al. 1995) to large mammals (Bascompte and Vilà 1997, Ferguson et al. 1998a, Ferguson et al. 1998b, Mouillot and Viale 2001). The fractal dimension (D) indexes the overall complexity of a movement path using a scale-independent measure of movement. The index of fractal dimension ranges from D=1 when an animal is moving along a perfectly linear path to D=2 when movement is extremely convoluted and essentially all points in two-dimensional space are visited (analogous to "Brownian-like" or random-walk paths) (Wiens et al. 1995). Fractal dimensions lie somewhere between these two extremes, with values for insects generally <1.5 and values for large mammals generally >1.5 (Ferguson et al. 1998b).

Recent advances in satellite tracking technology and the miniaturization of transmitters have enabled the collection of large amount of movement data from species inhabiting remote or inaccessible environments. In the case of marine predators such as the narwhal, extending landscape-based pattern metrics to the marine environment can identify important foraging zones, potentially even elucidating areas with unique or important oceanography. This study applied concepts in fractal geometry to quantify space-time related differences in the linearity of seasonal movement patterns of narwhals. Differences in sub-population specific movements were investigated across seasons and discussed in the context of causal factors or potential environmental heterogeneity encountered in the high Arctic.

METHODS

Location Data

Satellite location data were collected from three narwhal sub-populations in the eastern Canadian high Arctic and West Greenland. Studies were conducted in August 1993-94 in Melville Bay, West Greenland (Dietz and Heide-Jørgensen 1995, Heide-Jørgensen and Dietz 1995), August 1997-1999 in Tremblay Sound, Baffin Island, Canada (Dietz et al. 2001, Heide-Jørgensen et al. 2002a), and August 2000 in Creswell Bay, Somerset Island, Canada (Heide-Jørgensen et al., 2003a) (Figure 6.1). Narwhals were captured using nets set perpendicular to the shoreline (details on capturing and handling described in Dietz et al. 2001, Dietz and Heide-Jørgensen 1995, Heide-Jørgensen et al. 2002a).

Two types of tags were used: Telonics (Mesa, AZ) and Seimac (Canada) satellite-linked time depth recorders with approximately 0.5 watt power output; programmed and cast in epoxy by Wildlife Computers (Redmond, WA). Transmitters were attached to female whales 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). Whale movements were obtained using the ARGOS Data Location and Collection System (Harris et al. 1990). Tags transmitted ultra-high frequency messages, which were received by National Oceanic and Atmospheric Administration (NOAA) polar orbiting satellites. Locations were determined by Service ARGOS from the Doppler shift of the tag signal frequency that occurs during the satellite pass overhead (Harris et al., 1990). Only location classes 1, 2 and 3 (LC 1-3), which have a predicted standard error of 1.0, 0.35, and 0.15 km, respectively, were used in this analysis. None of the transmitters were duty-cycled.

Sex was determined by presence or absence of a tusk. Whales were classified into one of four size categories (category 1 = length <375 cm, category 2 = 375-424 cm, category 3 = 425-474 cm, and category 4 = $\geq$475 cm), one of three summering sub-populations (Melville Bay, Tremblay Sound, and Creswell Bay) based on tagging site, and one of two wintering grounds (Southern Wintering Ground and Northern Wintering Ground; Figure 6.1) based on wintering ground selection. The time series of data for each whale were divided into three seasons: summer period (tagging date to 15 September), migration period (16 September – 31 October), and winter period (1 November to end of tag transmissions).

Autocorrelation error, introduced by using pseudoreplicated locations in the analysis resulting from satellite passage and whale surfacing behavior, was addressed by selecting one good quality location from each 24-hour period. The daily position was selected by first visually examining the total number of positions for quantity and quality during each hour of the day for each whale. A 5-h time span was identified where position quality and quantity were highest from all tags. The mean minimum absolute difference was calculated between each hour in that time span and all ARGOS positions received for each individual. The hour with the smallest absolute difference, when averaged across all individual whales, was selected as the temporal point at which the closest daily position was selected.

Calculation of Fractal Dimension

Interest in behavioral changes by week and season provided the basis for selecting pathway length measurements and resulting fractal dimension calculations. The total pathway length was measured over seven different step lengths or measurement scales (in kilometers). Spatial step lengths were calculated incrementally for temporal step lengths of 1 day (using every sequential daily position) to 7 days (every 7th position or one per week). With increasing temporal step length, an increasing number of starting points for total distance calculations (different days) were available (e.g., for a step length of four, there were four different potential starting points for the calculation). For each of these cases (step lengths 2 through 7), total length measurements were calculated for all starting point options and the mean value for that temporal step length was used for each season. Calculations of fractal dimension was spatially and temporally restricted to narwhals within the study area for each season, with no more than a 7-day step length, to avoid the problem of scale dependence of movement pathways (Turchin 1996).

The fractal dimension (D) was derived by regressing the log of the measured length of pathway (L) on the log of the measurement scale (or step length) (δ) based on the power-law function:

$$L(\delta) = K * \delta^{1-D}$$

where K is the standardized length of movement pathways (km). The fractal dimension indexed the irregularity of movement paths over the range of measurement scales and K indexed the standard measure of pathway length. Fractal dimension and pathlength were calculated for individual whales for each of the three seasons. Data from each individual were pooled among years to assess overall seasonal patterns and data were then grouped based on sub-population, sex, size, or wintering ground to examine differences at the sub-population level. Fractal dimension was tested for normality and analyzed using two-way linear models in SPSS Version 11.0 with a significance level < 0.05.

RESULTS

Twenty narwhals (8 M and 12 F) were used in the analysis: Four whales (3 M and 1 F) from Melville Bay, West Greenland, 10 whales (5 M and 5 F) from Tremblay Sound, and 6 whales (6 F) from Creswell Bay (Table 6.1, Figure 6.1). Sixty-five percent of the whales were in size category 2 (375-424 cm), 15% in size category 3 (425-474), and 10% distributed in each of size categories 1 (<375) or 4 (>475). ARGOS position quantity and quality, on average, peaked between the hours of 12:00 and 18:00 (local time). The mean minimum absolute time difference was found between all positions received by the satellite and the hour of 15:00 (local time). This hour was consequently selected as the time at which the daily, best quality position (LC 1-3) was selected for each whale. Daily positions for all whales deviated from 15:00 by 2.04 h (SD 0.9).

Fractal dimension was normally distributed (Shapiro-Wilk statistic, $W=0.96$, $p=0.15$) and parametric statistics were used. The fractal dimension on measurement scales from 1 to 7 days showed self-similarity within the range of step lengths (Figure 6.2) and indicated that this range was acceptable for the assumption of scale-independence (Turchin 1996). Fractal dimension for individual whales ranged from a minimum of 1.15 (calculated during migration) to a maximum of 1.93 (calculated during summer) (Table 6.1).

Seasonal and annual differences

Estimated fractal dimensions for pooled individuals were 1.61 in the summer (SE 0.04, n=20), 1.34 during migration (SE 0.03, n=16), and 1.69 in the winter (SE 0.06, n=7), varying significantly across seasons ($F_{2,40}=15.92$, $p<0.001$). Tukey HSD post-hoc tests indicated this difference was due to the low fractal dimension during the migration period. The general pattern of seasonal movement and the seasonal fractal dimensions (Figure 6.2) were similar for almost all whales. Fractal dimension was significantly highest during the summer period, indicating the most irregular and random movements. Fractal dimension was significantly lowest during the migration period, indicating the most directed, linear movements. Fractal dimension increased significantly again in winter when whales reduced travel speed and remained in localized areas in the pack ice, to a value similar, to but not as high, as the summer (Figure 6.3). Standardized pathlengths could only be compared between individuals for summer and migration seasons, since tags that failed during the winter period did not record the entire movement pathlength for that season. The mean pathlength K for the summer season was 767 km (SD 496), less than half the mean pathlength for the migration period (1,801 km, SD 343).

Significant differences were found for fractal dimension between year and season ($F_{9,26}=5.38$, $p<0.001$), with post-hoc tests indicating differences occurring in summer and migration. Post-hoc analyses could not be conducted between all years or seasons because in 1997 there was only a sample of one. When Tukey post-hoc analyses were conduced for summer excluding the year 1997, significant differences were found for the fractal dimension in summer between both 1993 and 2000 and 1994 and 2000.

Sex and size category differences

There were no significant effects of size category or sex on the fractal dimension by season. The effect of size category in summer was, however, just above 0.05 (p= 0.07). This was due to two individuals in size class 1, which deviated from the observed general pattern for all other whales (ID 20691-99 and 7928-00). These two whales were the smallest in the sample (370 and 350 cm standard length), and presumably the youngest. They were tagged and tracked from two different summering grounds in 1999 and 2000. Both individuals had a delayed migration exploring alternative regions that were not visited by the rest of the population.

Sub-population and wintering ground differences

There were large differences in the fractal dimensions of movement between sub-populations across seasons (Table 6.1). The most convoluted path for whales from Melville Bay (D=1.86) occurred during the summer and movement patterns became more linear in the fall and winter (D=1.50 and D=1.51 respectively). Conversely, the most convoluted path for whales from Creswell Bay occurred during the winter (D=1.85) and fractal dimension was lowest during the migration (D=1.24) (Table 6.1). Tremblay Sound whales exhibited the least variation in fractal dimension across seasons, where fractal dimension was high on both the summer and wintering grounds (D=1.60-1.63) and lowest during migration (D=1.36).

Significant differences were found between seasons and sub-populations ($F_{4,34}$=10.60, p<0.001). During summer, narwhal movements on the summering ground in Melville Bay were significantly more convoluted than whales in both Tremblay Sound (p=0.01) and Creswell Bay (p<0.001). The difference between Tremblay Sound and Creswell Bay was not significant during summer (p=0.07). Differences in D were also found for the migration period. Melville Bay and Tremblay Sound had significantly lower fractal dimensions than Creswell Bay (p=0.003 and p=0.04, respectively) although Melville Bay and Tremblay Sound were not significantly different. During winter, where the two sub-populations from Melville Bay and Tremblay Sound share a wintering ground, their fractal dimensions were similar and not significant from one another. Both of these sub-populations had significantly lower fractal dimensions than the sub-population of whales from Creswell Bay wintering in an area further north (p=0.01 and p=0.04, respectively).

When whales occupying the two wintering grounds were pooled and examined for differences, fractal dimension was significantly different ($F_{1,5}$=22.05, p=0.005). The fractal dimension on the Northern Wintering Ground (whales from Creswell Bay) was higher (D=1.85, SE 0.07) than the fractal dimension on the Southern Wintering Ground (whales from Melville Bay and Tremblay Sound) (D=1.56, SE 0.06).

DISCUSSION

Meaningful quantitative descriptions of spatial pattern are important in ecology. Pattern metrics are frequently used methods to describe, simplify, or group complex spatial data into categories that are more easily understood or analyzed. It is, however, important that pattern analysis is not merely subjective but that the observed differences are quantified. Even though individual movement path parameters can easily be indexed (i.e., speed, distance, bearing), the mechanisms responsible for variation may not be easily understood and subjective behavioral grouping can confound the interpretation of results.

Turchin (1996) suggests fractal theory is not applicable to movement data due to a lack of self-similarity. Clearly, animal paths do not follow the pure definition of fractals, as clusters or breaks tend to define multiple realms of self-similarity in nature (Ferguson et al. 1998b). Studies have documented the hierarchical nature of marine species response to patch structure using spatial autocorrelation indices (Fauchald et al. 2000) indicating organisms may be responding to prey distribution or density on a range of nested scales. In this study, the range of measurement scales was restricted to one to seven days and temporal scales were investigated on the order of seasons. This is the range of scales over which fractal dimension would reflect short-term behavior and where patterns and causation are both recurring and predictable.

The fractal dimensions for seasonal narwhal movements are consistent with descriptions of behavior yet provide a metric for the qualitative patterns. Narwhals tend to have high fractal measures of movement during the summer when they occupy restricted localities. This follows well with summer behavioral descriptions of high site fidelity to coastal bays and fjords, with minimal to no long-distance exchange between sub-populations (Heide-Jørgensen et al. 2003a). The lowest fractal dimension (least complex behavior) was found during the migration period. The literature describing narwhal migration reports a substantial increase in daily travel distances and speed, together with a substantial decrease in the amount of time spent stationary in a single area (Dietz et al. 2001). In winter, the increase in fractal dimension was due to occupation of the wintering grounds, where whales remain stationary for up to 6 months during the continuous buildup of consolidated pack-ice. This also follows well with winter studies of localized horizontal and vertical ranging behavior.

The convoluted summer and winter pathways suggest that narwhals are interacting with environmental heterogeneity on a finer scale (Weins et al. 1995). The similarity in tortuosity, however, is likely driven by different factors during these seasons. The reasons for high summer site fidelity to localized bays and fjords are not completely understood. The summering grounds do not appear to afford large quantities of prey and intense feeding behavior has not been observed (Finley and Gibb 1982, Heide-Jørgensen et al. 1994, Laidre et al. 2002). These localized movements may be important for calves or may be a remnant of matrilineal site-specific behavior, similar to the beluga (*Delphinapterus leucas*), a close phylogenetic relative.

During the migration, the linearity of movement paths suggests individuals are not searching for highly clumped resources and are moving in a directed manner. The migratory period of narwhals is well defined; they leave their summering grounds in early to mid-September (prior to ice formation) and move in specific corridors towards offshore areas (Dietz et al. 2001, Heide-Jørgensen et al. 2002a). The timing of this migration is very specific, with whales moving out of the same areas on the same dates each year. Because of this strict schedule, narwhals have most likely adapted to a course that leaves little time for exploration of alternative regions along the way. There was some sub-population variation in the fractal dimension observed during the migration period, likely reflecting different paths (coastal or offshore) narwhals take towards their wintering grounds.

In winter, the localized movements can be primarily attributed to dense sea ice. Narwhals inhabiting pack ice are at the mercy of reliable leads and cracks for breathing as they are entirely dependent upon the physical structure of the ice and cannot break breathing holes (Siegstad and Heide-Jørgensen 1994, Heide-Jørgensen et al. 2002b). This consequently restricts narwhal movements to areas that are not completely closed and at the same time, requires whales shift with movements of leads. Localized movements on the wintering grounds are also likely influenced foraging behaviour (Laidre et al. 2003). Narwhals from West Greenland and the eastern Canadian high Arctic have a sympatric winter distribution with deep-water Greenland halibut (*Reinhardtius hippoglossoides*) in Baffin Bay, and there is evidence of significant and consistent predation on these halibut during winter (Chapter 5). The narwhals on the wintering grounds have limited options for long-distance movements to search for schools of squid or pelagic fish species because they are confined to small open water regions. Locations of high-density benthic prey on the wintering ground may enforce restricted horizontal movement and may be reflected in the fractal dimension.

The two smallest, and probably youngest, female whales were responsible for the deviations from the general fractal patterns or pathway lengths. When the standard date (15 September) for the end of summer was used for whale 20691-99 (tagged in Tremblay Sound, Baffin Island), it resulted in an exceptionally low fractal dimension (D=1.18). This was due to a delayed migration, where this whale traveled west to Admiralty Inlet, and then made localized movements until October 4 (see Heide-Jørgensen et al. 2002a). When this delayed migration was accounted for and summer date extended the fractal dimension rose to D=1.36. Another whale (7928-00 tagged in Creswell Bay, Somerset Island), traveled through Peel Sound following other whales from the sub-population in late August. However in September, it turned south and explored bays and fjords in Franklin Strait for an additional 3 weeks, while the rest of the sub-population from Creswell Bay migrated out through Lancaster Sound (see Heide-Jørgensen et al. 2003). Standardized pathway lengths for this individual were nearly identical in summer and migration due to the exceptionally long exploratory period (1,141 km vs. 1,161 km). Both of these behavioral deviations detected using fractals were qualitatively identified in the literature (Heide-Jørgensen et al. 2002a, and Heide-Jørgensen et al. 2003a). These deviations may be due to foraging inexperience or increased exploratory tendencies of younger individuals, if strict fidelity to movement paths and departure timing has not yet been formed.

The differences in fractal dimension between wintering grounds offer insight into movement patterns in response to sea ice. The whales occupying the Northern Wintering Ground displayed more convoluted paths than whales occupying the Southern Wintering Ground. The effect of sea ice (concentration, shifting leads and cracks, and flow size) is not uniform across Baffin Bay and conditions experienced by whales on different wintering grounds vary. A wider range of sea ice concentrations and larger fractions of open water have been detected on the Southern Wintering Ground based on analysis of remotely-sensed microwave sea ice data between 1978-2001 (Chapter 7). This may be due to the closer location of the Southern Wintering Ground to the pack ice edge, where conditions are more dynamic and offer whales greater freedom of movement. Narwhals may need to travel greater distances to keep up with shifting leads and cracks, which is reflected in a lower fractal dimension in this area (Chapter 7).

Observing how an organism responds to the structural complexity of the environment and how this response is modified on different time scales can provide information on the mechanisms of interaction with landscape structure and the spatial response of a population to dynamic processes (With 1994, Wiens et al. 1995). The application of fractal dimension to examine movement data for a marine mammal is a non-traditional method and can be extended to comparative analyses or interpretations of life history patterns. The method offers an objective means for using behavior to identify areas of particular geographic interest (i.e., foraging, breeding). The major prospect for fractal analysis of movements lies in the comparative nature of the metric for identifying changes over time between species, populations, or smaller groups inhabiting similar habitats. The fractal dimension can be viewed as the species' or populations' strategy for dealing with spatial and temporal changes or response to environmental heterogeneity. Comparison between narwhals and other Arctic marine mammals will provide insight into the dynamics of the Arctic environment and strategies that determine viability of species under the influence of climatic change.

Table 6.1. Fractal dimensions for paths of individual narwhals in three seasons for three sub-populations in Melville Bay, Tremblay Sound, and Creswell Bay. Length is standard body length in cm. Standard deviation (SD) is reported in parentheses.

Sub-population	**ID-Year**	**Sex**	**Length**	**Summer**	**Migration**	**Winter**
Melville Bay	3960-93	M	>400	1.93	1.42	1.55
	20162-93	M	475	1.81	-	-
	20167-94	M	405	1.92	1.59	1.48
	20690-94	F	>400	1.81	-	-
All Melville Bay whales (N=4, 2, 2)				1.86 (0.05)	1.50 (0.08)	1.51 (0.08)
Tremblay Sound	6335-97	M	440	1.80	1.32	-
	3961-98	M	500	1.64	1.37	-
	20162-98	M	475	1.55	1.30	1.58
	20696-98	F	380	1.80	1.52	-
	3964-99	M	410	1.62	1.43	1.68
	20688-99	F	415	1.46	1.33	-
	20689-99	F	405	1.63	1.33	-
	20687-99	F	390	1.70	1.31	-
	20168-99	M	440	1.53	1.36	-
	20691-99	F	350	1.36	-	-
All Tremblay Sound whales (N=10, 9, 2)				1.60 (0.03)	1.36 (0.03)	1.63 (0.07)
Creswell Bay	20690-00	F	398	1.53	1.23	-
	20689-00	F	397	1.38	1.28	1.91
	20688-00	F	402	1.56	1.34	1.78
	20683-00	F	390	1.17	1.23	-
	7927-00	F	390	1.56	1.15	1.87
	7928-00	F	370	1.47	-	-
All Creswell Bay whales (N=6, 5, 3)				1.44 (0.04)	1.24 (0.05)	1.85 (0.06)
All tracked whales (N=20, 16, 7)				1.61 (0.04)	1.34 (0.03)	1.69 (0.06)

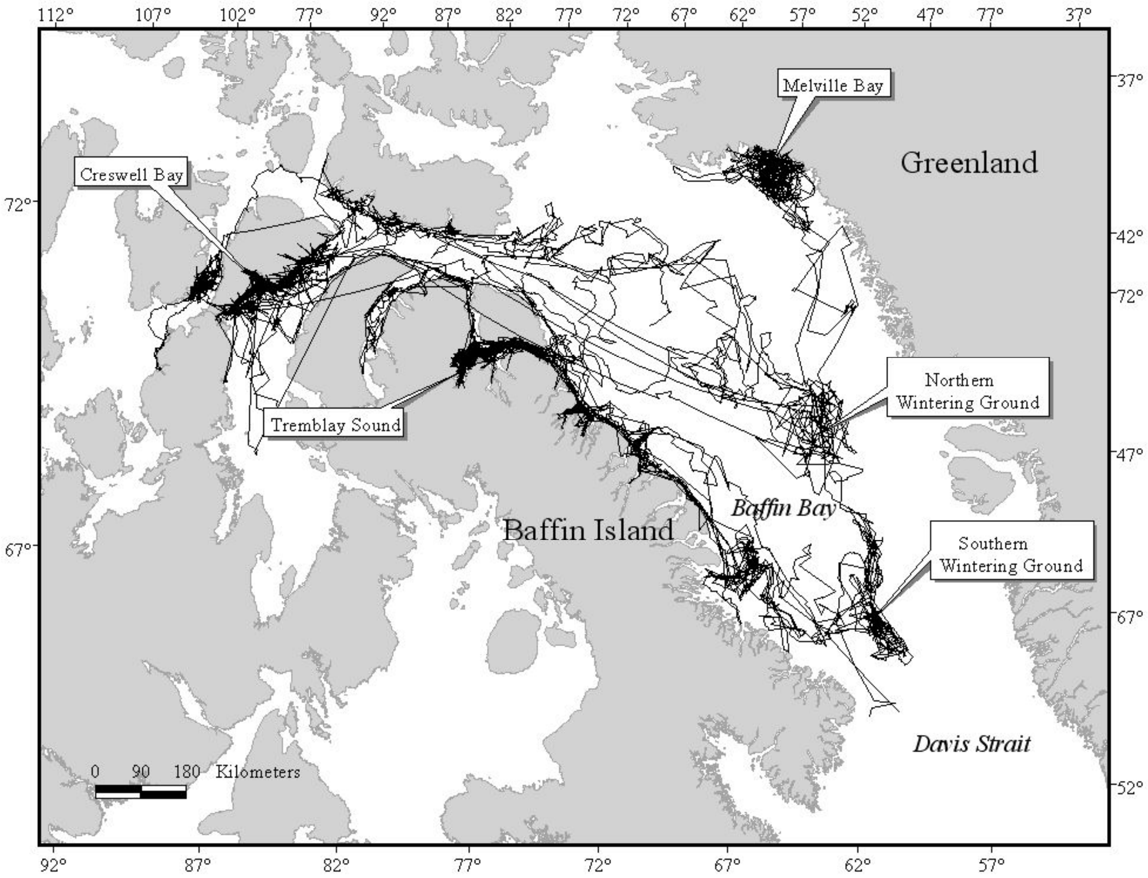


Figure 6.1. Movement paths created from ARGOS satellite location data for narwhals tagged at three summering localities (Creswell Bay, Tremblay Sound and Melville Bay) in Canada and Greenland.

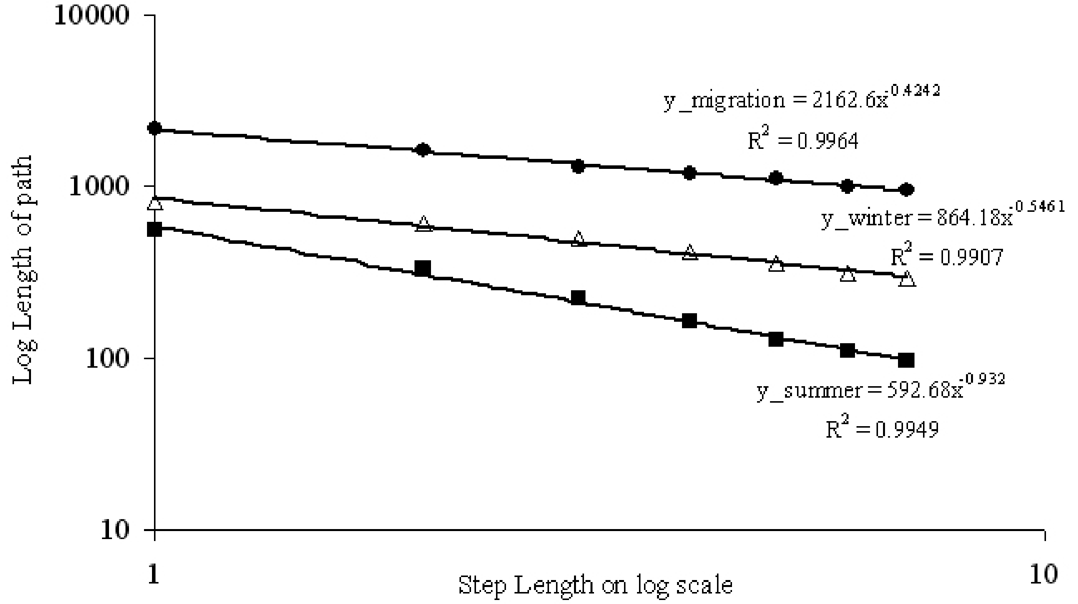
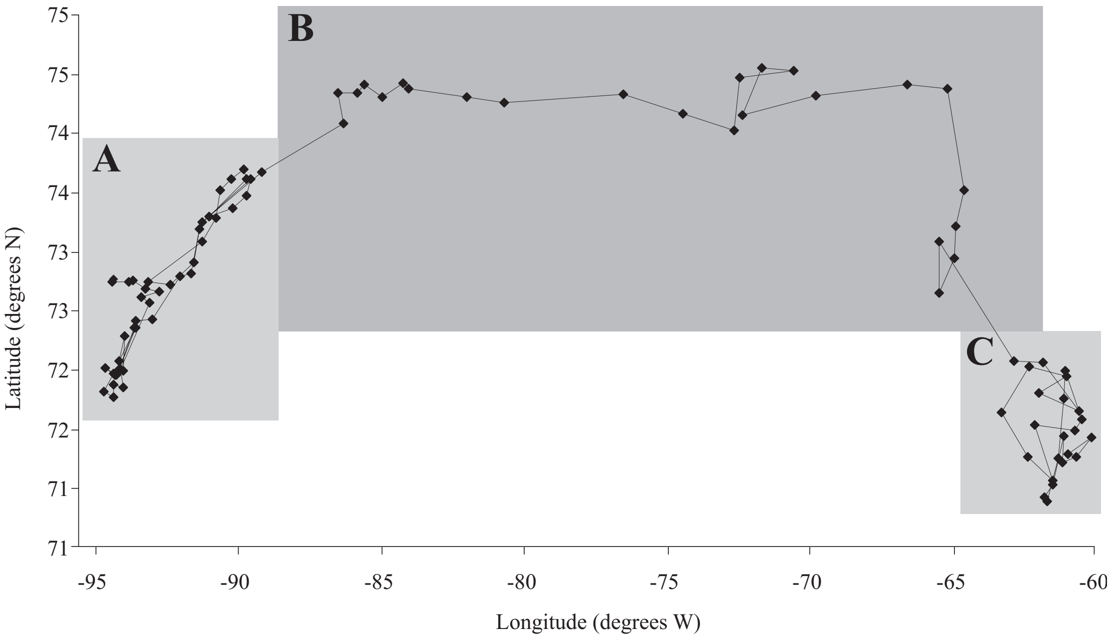


Figure 6.2. Regression between step length (km/day) and length of path (km) for a narwhal tagged in summer in Melville Bay, West Greenland in 1993 (ID 3960). The fractal dimension D = 1-exponent of *x* and K is the y-intercept. Fractal dimensions for this animal were D=1.93 (summer), D=1.42 (migration), and D=1.55 (winter). Note the longest path length was recorded during the migration period. The data for each step length by season are solid squares for summer, solid circles for migration, and open triangles for winter. Similar regressions were conducted for each season for each individual whale.



Figures 6.3. Entire movement pathway of narwhal ID 20689, tagged in Creswell Bay in 2000, shown with daily positions as black markers. Seasonal fractal dimensions for each pathway were A) summer (D = 1.38), B) migration (D = 1.28), and C) winter (D = 1.91). Note, data are shown on an unprojeted scale and are intended to illustrate movement behavior in different seasons.

CHAPTER 7
ARCTIC SEA ICE TRENDS AND NARWHAL VULNERABILITY

INTRODUCTION

Significant physical and biological shifts have recently been reported for polar environments and are attributed to pervasive alterations in the global climate (Murphy and King 1997, Morison et al. 2000, Wigley and Raper 2001, Parmesan and Yohe 2003, Root et al. 2003). In the past 25 years, the hemispheric extent of annual sea ice in the Arctic has decreased by 3% per decade, with perennial sea ice decreasing at 9% per decade (Johannessen et al. 1999, Vinnikov et al. 1999, Parkinson et al. 1999, Parkinson and Cavalieri 2002, Comiso 2002). Combined with these sea ice trends are reports of changing salinity, warmer air and water temperatures (Morison et al. 2000, Wigley and Raper 2001), shifts in thermohaline circulation (Morison et al. 2000, Mysak 2001), and reorganization of marine zooplankton communities (Beaugrand et al. 2002), all of which leave growing scientific consensus that the Arctic climate is undergoing considerable change.

There have been rampant speculations about how global climate change will impact top Arctic predators. Arctic marine predator movement and life history can generally be linked to the cyclical nature of sea ice. Consequently, many studies predict nutritional stress due redistribution of prey, changes in survivorship or fecundity, and shifts in migrations due to changing ice patterns. Conservation measures focused on population response have been hampered by insufficient data on polar amplification of warming trends, incomplete information on species distributions and life history traits, and non-uniform or region-specific patterns. A unifying feature of nearly all of climate change studies is the focus on warming trends and concurrent increasing temperatures or decreasing sea ice in areas such as Alaska (USA) and Hudson Bay (Canada) (Stirling and Derocher 1993, Tynan and DeMaster 1997, Stirling 1997).

While due attention has been given to the hemispheric warming trends, recent work indicates that patterns of climate-induced change must be examined on regional scales. Studies in the Canadian high Arctic, Baffin Bay, and West Greenland report findings that are markedly different from the overall trends of sea ice reduction. Since 1970, the climate in West Greenland has cooled, reflected in both oceanographic and biological conditions (Hanna and Cappelen 2003). Contrary to a reduction of sea ice, Baffin Bay and Davis Strait display strongly significant increasing tends in ice concentrations and extent, as high as 7.5% per decade between 1979-1996, with comparable increases detected back to 1953 (Parkinson et al. 1999, Deser et al. 2000, Parkinson 2000a, Parkinson 2000b, Parkinson and Cavalieri 2002, Stern and Heide-Jørgensen 2003).

Almost no data exist to determine the effects of increasing sea ice concentration on Arctic cetaceans, as they occupy inaccessible habitats for most of the year and are not easily observed without the use of remote telemetry. Among the cetaceans that inhabit the Baffin Bay pack ice, the narwhal is perhaps the most conspicuous and offers a unique opportunity for examining effects of climate-induced sea ice trends. By far, the largest numbers of narwhals worldwide are found in Baffin Bay. They make extensive annual migrations from high Arctic summering grounds to low Arctic wintering grounds, where approximately 50,000 whales overwinter in the dense pack ice between November and April (Koski and Davis 1994, Innes et al. 2002, Heide-Jørgensen et al. 2002a, Heide-Jørgensen et al. 2003a). Narwhals arrive predictably on the wintering grounds between the end of October and 10 November (Dietz and Heide-Jørgensen 1995, Heide-Jørgensen et al. 2002a, Heide-Jørgensen et al. 2003a) and, to date, satellite tracking studies show that three sub-populations utilize two spatially distinct wintering grounds between which no overlap or exchange occurs (Heide-Jørgensen et al. 2003a). The wintering grounds are critically important for narwhal energy intake and overall fitness. Intensive feeding behavior has been documented during the 6-month period of residency suggests a major portion of the annual energy intake for narwhals is obtained in Baffin Bay in winter, in contrast to little feeding activity during the summer (Chapter 5, Laidre et al. 2003).

Narwhals require leads and cracks in the ice to breathe and cannot maintain open breathing holes. There have been no direct observations of narwhal mortality in the pack-ice in central Baffin Bay, as the area is hundreds of kilometers from shore and rarely visited by humans. There are, however, numerous reports of large-scale mortality events of narwhals in coastal pack-ice, where sudden changes in weather conditions cause rapid freeze up of leads and cracks eliminating access to air for breathing (Siegstad and Heide-Jørgensen 1994, Heide-Jørgensen et al. 2002b). Due to this documented vulnerability, reductions in the availability of open water in the Baffin Bay pack ice may have deleterious consequences for these uniquely-adapted marine mammals.

In light of overall increasing sea ice in Baffin Bay and in terms of incorporating climate change vulnerability into population risk assessment, it is necessary to examine local trends in the fraction of open water on narwhal wintering grounds. The objectives of this study were to examine interannual and intraannual trends in the ice concentrations and fraction of open water on the wintering grounds of narwhals using a 23-year time series of satellite-derived data on ice conditions between 1979-2001. Information on sub-population specific area use was used to determine if region-wide trends in sea ice reported for Baffin Bay and North Davis Strait could be detected at the narwhal winter habitats. This information was coupled with known anthropogenic impacts and conservations measures discussed.

METHODS

Sea Ice

Sea ice data were obtained from the National Snow and Ice Data Center (NSIDC) in Boulder, Colorado, USA for all available days between 26 October 1978 and 9 September 2001. The data set included passive brightness temperatures from both the Scanning Multichannel Microwave Radiometer (SSMR, every second day between 1979-1987) and the Special Sensor Microwave Imager (SSMI, daily on several satellites since 1987). The sharp contrast in microwave emissions between the sea ice and the open water, together with the relative absence of atmospheric interferences with the microwave signal, allowed for the calculation of the sea ice edge location and the approximate sea ice concentrations within the ice pack. Sea ice concentration (1% resolution) was derived using the Bootstrap algorithm following Comiso (1995), where daily sea ice concentrations for the Northern Hemisphere were mapped to a polar stereographic projection (true at 70^oN) at a 25 kilometer resolution. Sea ice data obtained from the NSIDC were converted from raw binary to ASCII format and daily data were imported to a geographic information system (GIS, ESRI ArcINFO 8.3) as raster grids, where the center of each cell received the estimate of average sea ice concentration in that 625 km^2 area. Daily ice grids were clipped to a predefined study area of interest (Figure 7.1), which included the full spatial extent of both the northern and southern narwhal sub-population wintering grounds.

Narwhal wintering grounds

Spatial delineation of wintering grounds for each sub-population was based on 95% kernel probability area estimates derived from the satellite tracking geographic data (Heide-Jørgensen et al. 2002a, Heide-Jørgensen et al. 2003a). Polygon home range estimates were converted into the raster data format and used as a spatial mask to extract sea ice data for these regions on a daily basis. The sub-population of narwhals from Somerset Island, Canada occupies the northern wintering ground (NWG) in central Baffin Bay. This area was estimated to be

25,486 km^2, or approximately 40 pixels. The sub-populations from Melville Bay, West Greenland and Eclipse Sound, Canada occupy the southern wintering ground (SWG), an area estimated as 23,125 km^2, or 37 pixels.

Spatial and temporal analysis

A sample dataset was created by selecting the daily grids of the 1st and 15th day of each month (November through April) of each year of the time series for only those cells defining the home range of both sub-populations. When necessary (due to missing data) the 2nd or 16th days of each month were used as substitutes. The fraction of open water and total area of open water (km^2) on each wintering ground (variables describing ‘ice-free’ area within the ice pack) were calculated for each of the 12 observations within the time series. The fraction of open water on the wintering ground (*F*) was modeled as:

$$F = \left(\sum_{i=1}^{h} (PC_t * (1 - (IC_t / 100))) \right) / WGA$$

where *i* indexes the lowest sea ice concentration on the wintering ground for a given time *t* to *h*, the highest sea ice concentration, *IC* is specific sea ice concentration calculated in full integer units and recorded as a percent, *PC* is pixel count for each specific sea ice concentration, and *WGA* is the wintering ground area in number of pixels. The area of open water (A) for a given time step was then *PA*F*WGA*, where *PA* is pixel area (625 sq km).

Maximum ice concentration was found to occur most frequently in the month of March for both wintering grounds. To explore the variation in the maximum ice concentration over time, a monthly mean time series for March (referred to as the March composite) was created for each year. The March composite was a product of the vertical spatial and temporal average ice concentration for each cell for all days in March. A 5-year moving average of the variance of the residuals between 1978-2001 was calculated for the March composite to elucidate interannual variability in the minimum amount of open water on the wintering grounds. Trends in sea ice were calculated as the slope of a line of best fit to each time series using a standard least squares procedure. The significance of the slope was estimated based on a standard F-test. Autocorrelation in the time series was calculated out to 5-year lags for each observation point to examine interannual correlation.

RESULTS

Intraannual variability

The range of sea ice concentrations and the fraction of open water varied widely between November and April on both wintering grounds (Table 7.1). The most rapid growth of sea ice and the greatest variability occurred during the early months of the narwhal residency period (November and December). When whales arrived on the wintering grounds, average ice concentrations ranged between 29% (SD 20) and 69% (SD 26), with typically >60% of the wintering ground being ice-free (Table 7.1).

The available open water declined rapidly between 1 November and 15 December. Freeze-up was faster on the NWG, where on any given date there were generally higher concentrations of sea ice and less open water. The rapid decline in open water slowed as 1 January approached, and by 15 January less than 5% open water was present on both wintering grounds (Figure 7.2). The fraction of open water continued to slowly decline through February and conditions reached a minima of 0.5% open water on the NWG at the end of March (on average 132 km^2 out of a 25,000 km^2) and 1.9% open water on the SWG at the same time (438 km^2 out of 23,125 km^2).

The average ice concentration between 15 January and 15 April was typically about 97% (SD 2-3) for both wintering grounds. Concentrations typically reached lower minima on the SWG (85%) than the NWG (92%) (Table 7.1). The SWG consistently contained a 2 – 3 times larger fraction of open water than the NWG, on average 450-650 km^2 between 15 January and 15 April (Figure 7.2). There was no evidence of an increase in open water availability on 15 April on either wintering ground, the time when whales initiate the spring migration north to the summering grounds. All trends in fraction of open water on the NWG between 15 February and 15 April suggested decreasing open water, and declining trends on 15 February and 15 March were significant at the 99% confidence level. No significant trends were found on the SWG for any observation period.

Interannual variability

There was high year-to-year variability in the 22-year time series in both wintering grounds even though values for the fraction of open water generally remained below 5% during winter (Figs 7.3 a and b). Autocorrelation indices, examined out to 5-year lags, did not suggest temporal correlation for any given observation in either wintering ground. Autocorrelation coefficients for a 1-year lag ranged from 0.07 to 0.4 and beyond one year, no clear patterns emerged. Open water availability was at its lowest in winters of 1986-87, 1992-93, 1996-97 and 2001, with cyclical changes across several years most pronounced on the NWG and during the early period of residency between November and December. The pattern of open water variability followed region-wide Baffin Bay cyclical patterns reported in previous studies.

Changes in maximum area of open water

The area of open water calculated for the March composite ranged from 75 to 619 km^2 and 319 to 1,081 km^2 in the NWG and SWG, respectively. Linear models fit to monthly March averages produced a significant decreasing trend in the fraction of open water on the NWG with a slope of –0.04% per year (SE 0.02) ($p=0.02$, $r^2=0.22$) and a decreasing trend but not significant on the SWG with a slope of –0.01% per year (SE 0.02) (Figs 7.4 and 7.5). There was a strong increasing significant trend (0.03% per year, SE 0.006) in the variance of the 5-year running average of the residuals for average conditions in March ($p<0.001$) in the NWG (Figure 7.4). In the SWG, the trend in variance of the residuals was also increasing however was not significant (Figure 7.5). The amount of open water on the NWG measured for the March composite varied by a factor of 2 within on year.

DISCUSSION

Satellite tracking studies show that narwhals arrive on the wintering grounds in Baffin Bay no later than 10 November (Heide-Jørgensen et al. 2002a, Heide-Jørgensen et al. 2003a). The results from this analysis suggest that obstruction by sea ice does not influence when or where whales terminate their migration, as the wintering grounds are >60% open water when whales arrive and begin localized movements. Apparently whales use alternative cues to locate wintering grounds and do not cease their migration due to barriers created by ice. This is intriguing relative to patterns of narwhal site fidelity, as whales return to the same regions in central Baffin Bay year after year where identifying landmarks are not available. This also has important implications for timing and pace of freeze-up around the wintering ground in December.

The extreme minimal amount of open water availability during March indicates narwhals are highly adapted to successful existence in pack ice. No other cetacean has been demonstrated to occupy such dense winter sea ice cover for such a long period of time. The fraction of open water available to whales between 1 February and 15 April was no more than 5% on both wintering grounds. Despite this restriction, narwhals manage to make relatively large daily movements during this time, up to 40 km per day in some months (Heide-Jørgensen et al. 2002a). Fractal dimensions of movement illustrate that whales on the Northern Wintering Ground have more convoluted movements (lower fractal dimensions) than whales on the Southern Wintering Ground, which make more linear movements (higher fractal dimensions) (Chapter 6). It may be appropriate to speculate that these movements reflect sea ice conditions in the two areas. It is possible whales on the Southern Wintering Ground have greater freedom to make linear movements with more open water access or move larger distances to keep up with shifting leads and cracks. Whales on the Northern Wintering Ground alternatively may face more restrictive or constant sea ice conditions and must remain localized, excluded from longer-distance movements.

Local decreasing trends in the fraction of open water were detected on both narwhal wintering grounds in Baffin Bay. Although trends were similar on the Southern Wintering Ground, they were not detected with the same strength as on the Northern Wintering Ground, significant at the 95% level or higher. The non-significant trend on the Southern Wintering Ground may be caused by its closer proximity to the pack ice edge or large open water areas in Davis Strait. The compelling evidence of declining open water in March confirms that winter pack ice conditions experienced by narwhals are in transition and fewer leads and cracks are available for access to air. Over the 23-year time series investigated here, the cyclical nature of the availability of open water on the wintering grounds followed cyclical patterns observed in region-wide Baffin Bay (Parkinson 1995, Parkinson et al. 1999, Stern and Heide-Jørgensen 2003). Consequently, it appears that large-scale trends detected for Baffin Bay and Davis Strait may be good indicators of trends in localized and restricted narwhal habitats.

Often spatial resolution must be sacrificed for the sake of temporal continuity in remotely-sensed data series. The estimate of 0% open water on the wintering grounds for some years (Figures 7.3a and b) is an artifact of low spatial resolution. It is likely that in some years, open areas on the wintering grounds are so negligible that the SSMR/SSMI satellites cannot sense them. The error estimated by the NSIDC for ice concentration ranges from 5-10% and spatially averaging pixels for the March composite examination of open water trends generally reduced the impact of the error in the estimates. Regardless of resolution, the estimates indicate narwhals are severely restricted to few leads and cracks during winter and the open water on which they rely may only be detected by very high-resolution imagery (Figure 7.6).

There are great uncertainties in cetacean response to climate-induced perturbations. Cetacean occurrence is generally negatively correlated with dense or complete ice cover due to requirements for access to air. In dense ice, cetaceans rely on the availability of open leads and cracks and cannot enter regions where open water is unavailable or highly unpredictable. In the case of a pagophilic species with high site fidelity such as the narwhal, increasing ice may be lethal if open water accessibility declines beyond the minimum threshold which can be tolerated. Increasing sea ice may also affect prey availability, as the timing of primary and secondary production blooms occurs in concert with cetacean seasonal feeding patterns. Furthermore, increasing ice may block access to particularly favorable foraging areas. There are few documented effects of climate change on Arctic cetaceans in the scientific literature, and of those, most come from Alaska where sea ice is decreasing, Alaska case studies include altered migration timing (Johnson et al. 1981), shift in seasonal distributions (Moore et al. 2000, Moore 2000), and altered timing of life history events (Perryman et al. 2002).

The three year-round occupants of Arctic waters, the narwhal, beluga (*Delphinapterus leucas*), and bowhead whale (*Balaena mysticetus*), are listed as vulnerable to climate-induced perturbations by the International Whaling Commission (IWC 1997). Of these, narwhals are likely most vulnerable to changes in open water accessibility as they have the most restricted distribution and extreme high site fidelity to summering grounds, wintering grounds, and migratory routes. The beluga whale has been found in a range of ice types (Suydam et al. 2001, Moore 2000), but usually avoid dense pack ice (Barber et al. 2001) by wintering in open water polynyas or loose ice (Richard et al. 2001, Heide-Jørgensen et al. 2003b). Bowhead whales prefer floe edge habitat and are nevertheless capable of breaking holes through several feet of ice. Knowledge about bowhead whale distribution and movement plasticity indicates that their dependence on open water is not entirely critical to survival (Moore et al. 2000, Heide-Jørgensen et al. 2003c). Lacking the ability to break holes in the ice and preferring dense pack ice for 50% of the year, narwhals are at the mercy of open water availability. This vulnerability has been demonstrated by many ice entrapment events where hundreds of narwhals were trapped and killed during rapid sea ice formation caused by sudden cold periods (Siegstad and Heide-Jørgensen 1994, Heide-Jørgensen et al. 2002b).

The increasing trends in variability, in concert with the decreasing trends in the fraction of open water, provide insight into the annual conditions experienced by narwhals. Given that an optimal strategy for narwhals to persist in increasing winter sea ice cover would be to develop a learned behavior of adjusting to sea ice changes and moving south to more open areas, it would be imperative that whales could track changes in their habitat. Unfortunately, in light of the high and increasing interannual variability in the period with maximum ice cover, whales may not receive the necessary stimuli to perceive overall trends and adjust behavior accordingly. Additionally, timely behavioral adjustments to increasing sea ice require compensatory movements perhaps as early as December, before the whales are enclosed by expanses of dense pack ice leaving them few options for re-distribution.

Narwhals feed intensively on their wintering grounds and a major portion of their annual food intake is obtained in these areas (Chapters 4 and 5). Narwhals primarily take Greenland halibut (*Reinhardtius hippoglossoides*) although the diet also includes other species. During winter narwhals are highly restricted in the horizontal range of their movements and food intake must occur over a limited geographic range, a range which may be reduced by increasing sea ice. Recently, offshore Greenland halibut fishery operations were started in central Baffin Bay (Treble and Bowering 2002). The fishery is conducted during the open water period but in the precise geographic areas where narwhals spend the winter (Chapter 5). A reduced Greenland halibut abundance due to a commercial fishery, together with increased restriction on winter dispersal, will likely influence narwhal foraging success and may even reduce the carrying capacity for narwhals on the wintering grounds.

Narwhals are hunted intensively in Greenland and the Canadian high Arctic. Presently there are few restrictions on the harvest and no quotas have been established based on the determination that the annual harvest is sustainable (NAMMCO 2001). With increasing hunting effort due to larger human populations and improved technology, it will be necessary to enforce more restricted harvest regulations based on estimates of population size and maximum net production (Heide-Jørgensen In Press). Climate change, trends in Baffin Bay pack ice, and narwhal site fidelity are inevitable under any conservation strategy. Reduced abundance due to increased pack-ice mortality or nutritional deficiency is difficult to detect due to the low level of precision obtained even in intensive narwhal population surveys (Innes et al. 2002, Koski and Davis 1994, Heide-Jørgensen In press). Following the results from this study, estimates of maximum sustainable yield levels should also to include the risks of sudden large-scale mortalities on the wintering grounds. Further studies should be undertaken to examine the risk of ice entrapment events.

It is unknown if narwhals can adapt to long-term environmental changes by altering their extreme site fidelity. This species has not displayed this propensity previously, as narwhals repeatedly use the same migratory corridors and summering localities despite intense Inuit hunts, and return to the same areas despite the occurrence of ice entrapments. The marked consistency in annual movement patterns between sub-populations suggests a learned behavior, probably maternally-inherited and evolutionarily driven. Their movements may reflect behavioral traits that have proven successful over centuries or larger time scales, although not necessarily optimal in each year. Given narwhals profound dependence on the wintering grounds for energy intake, their reliance on a limited number of winter prey species, and their restricted range, they are vulnerable to negative perturbations from climate change. With the evidence of ominous changes in sea ice conditions that could impact foraging, prey availability, and of utmost importance, oxygen accessibility, it is unclear how narwhal sub-populations will fare in light of changes in the high Arctic.

Table 7.1. Average sea ice concentration and range (in 1% resolution) in the two wintering grounds for each observation between 1 November and 15 April. Sea ice concentrations were averaged across 1978-2001.

Observation	**NWG mean (SD)**	**NWG range**	**SWG mean (SD)**	**SWG range**
1 November	54 (31)	0-100	29 (20)	0-80
15 November	69 (26)	0-100	54 (27)	0-100
1 December	86 (16)	0-100	77 (22)	0-100
15 December	87 (20)	13-100	82 (19)	16-100
1 January	91 (13)	30-100	91 (12)	33-100
15 January	97 (2)	92-100	95 (7)	57-100
1 February	97 (2)	92-100	95 (6)	50-100
15 February	98 (2)	93-100	97 (3)	89-100
1 March	97 (2)	92-100	96 (3)	85-100
15 March	97 (2)	93-100	97 (3)	89-100
1 April	98 (2)	93-100	97 (3)	85-100
15 April	97 (2)	92-100	97 (3)	86-100

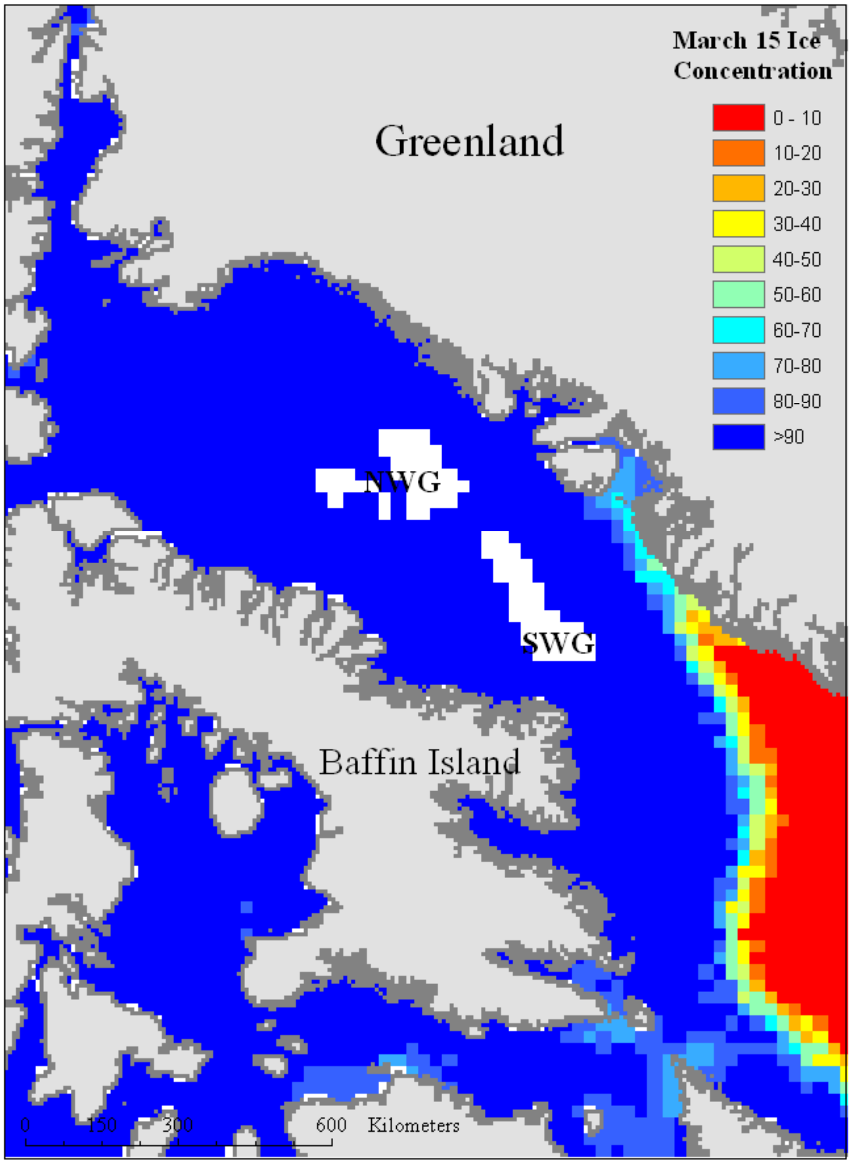


Figure 7.1. Map of study region showing example of March 15 sea ice cover (taken from 2001) and the locations of the NWG and SWG. Pixels were 25 x 25 km^2.

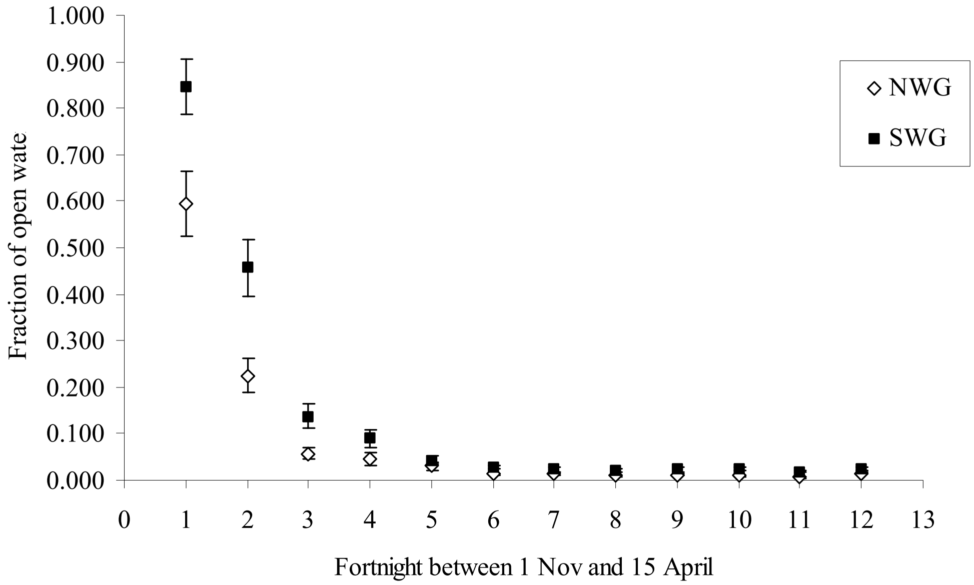
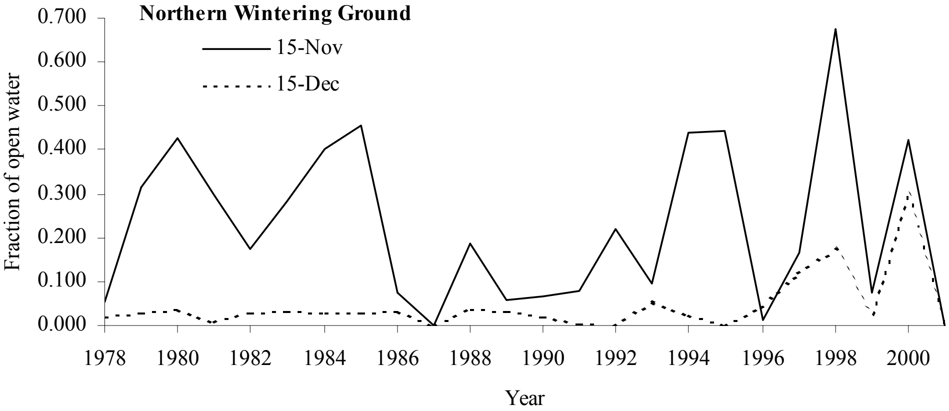
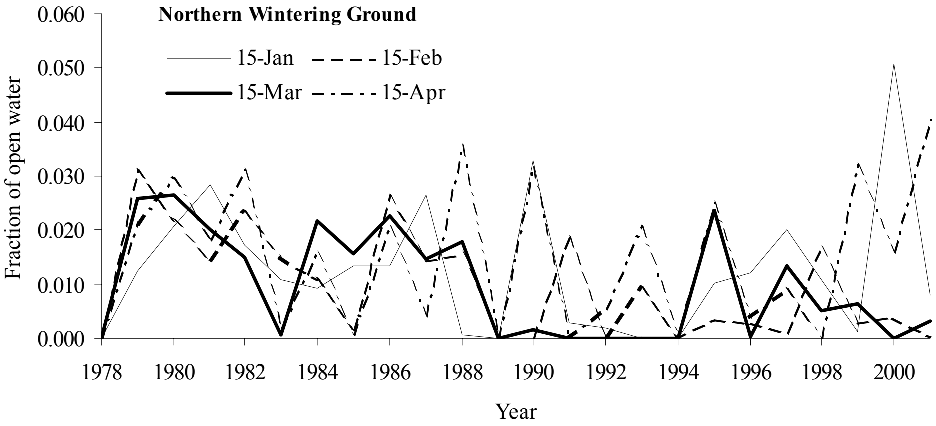
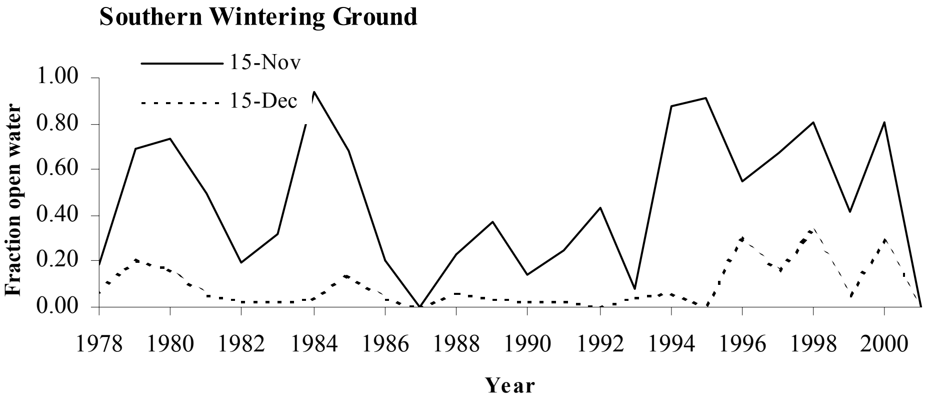


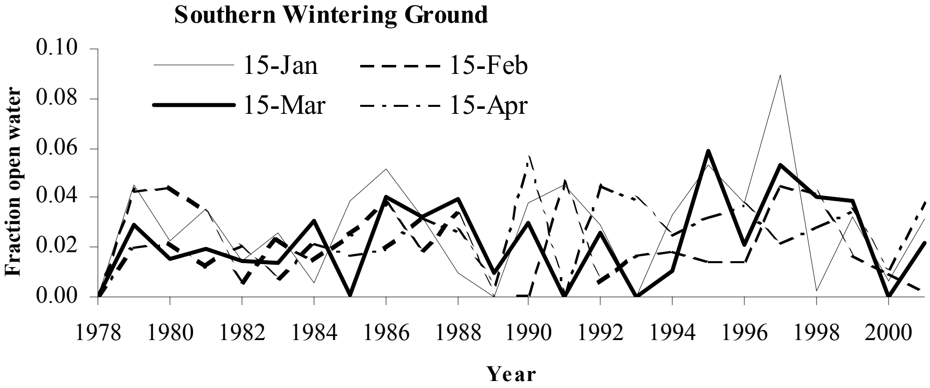
Figure 7.2. Average fraction of water (+/- SE) on the wintering grounds in two-week intervals between November 1 and April 15, 1978-2001.





Figures 7.3. a-b. Monthly fraction of open water on the NWG, shown in two graphs for each area for the 15th day of each month between November and April, 1978-2001.





Figures 7.3. c-d. Monthly fraction of open water on the SWG, shown in two graphs for each area for the 15th day of each month between November and April, 1978-2001.

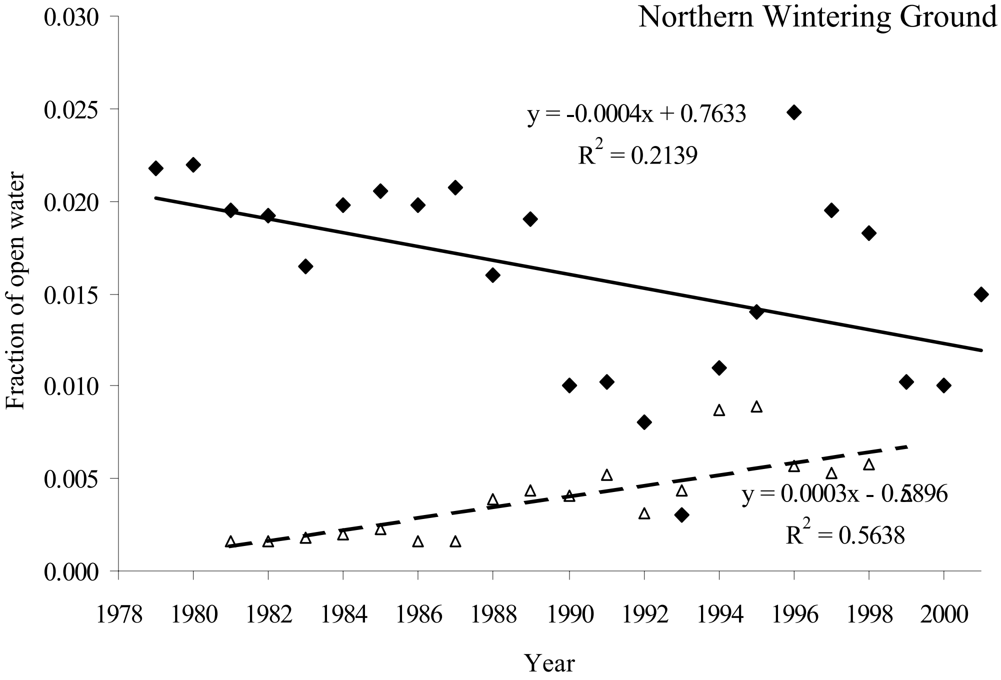


Figure 7.4. Trend in the average fraction of open water on the Northern Wintering Ground based on annual estimates of average March sea ice concentrations (solid symbols represent measure of the fraction available each year with solid trend line). A 5-year running average of the variance of the residuals shows an increasing trend (open symbols and dashed line). Both trends were highly significant at or above the 95% confidence level.

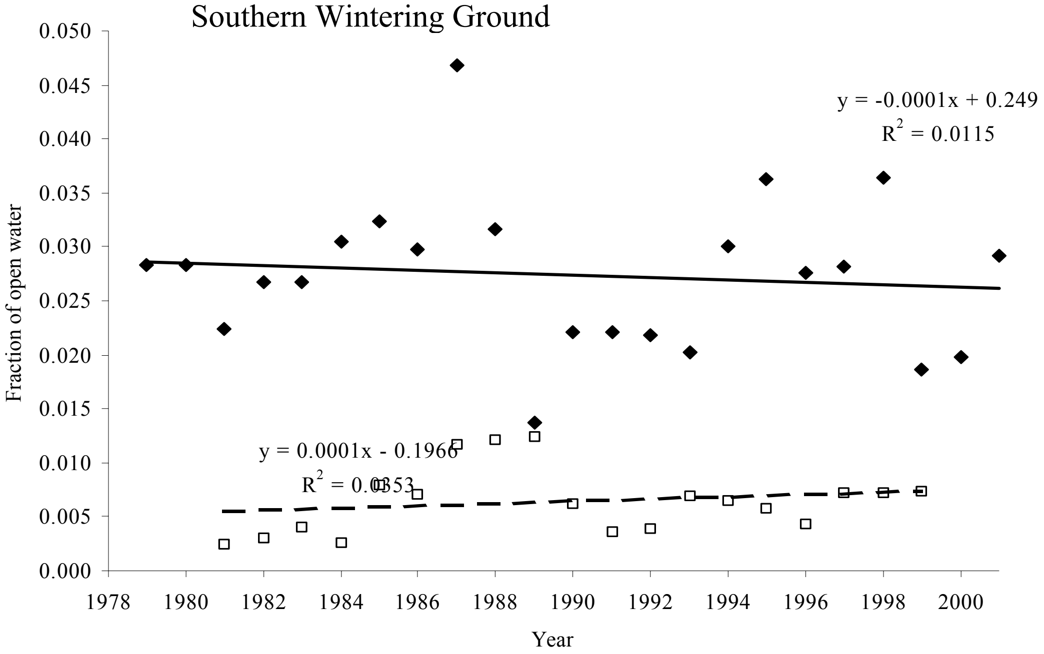


Figure 7.5. Trend in the average fraction of open water on the Southern Wintering Ground based on annual estimates of the average March sea ice concentrations (solid symbols represent measure of the fraction each year with solid trend line). A 5-year running average of the variance of the residuals shows a sight-increasing trend (open symbols and dashed line) however neither trend was significant.

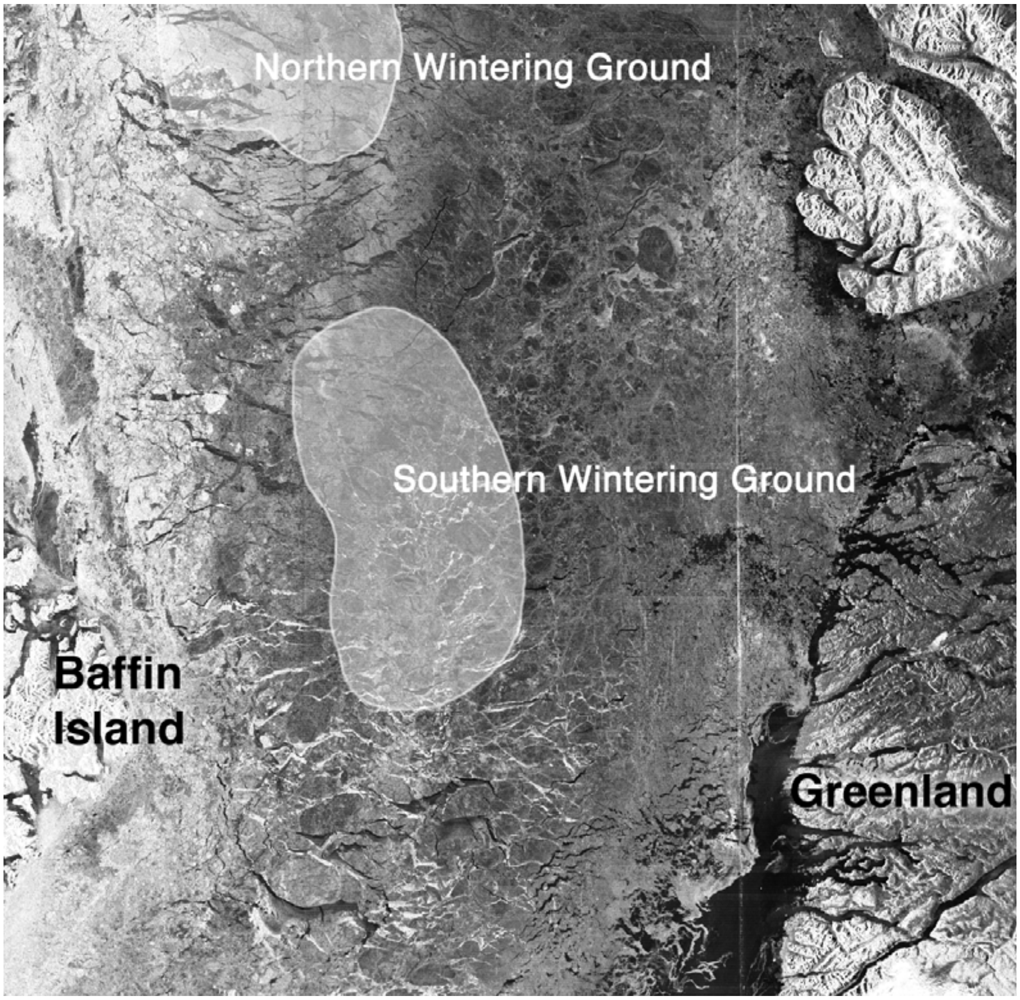


Figure 7.6. RADARSAT satellite image of sea ice concentration in Baffin Bay on 17 February 1999. Note the location of the two narwhal wintering grounds and minimal leads and cracks available in the area.

CHAPTER 8

SEASONAL NARWHAL HABITAT ASSOCIATIONS IN ARCTIC WATERS

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. Animals 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, Gregr and Trites 2001, Carroll et al. 2003). 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 both an animal's location in space and time and a measure of the animal'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 attracting 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 fundamental processes characterizing important foraging regions.

In the case of the 3-dimensional marine environment, one of the few ways of deriving behavioral metrics is the use of remote telemetry. One of the most common telemetry devices used on marine megafauna is the satellite-linked time depth recorder (SLTDR). These instruments provide multiple daily geographic positions based on Doppler shift of tag transmissions when animals are at the surface and binned dive data recording dive depths, dive durations, and time at depth summarized in four 6-hour periods (Heide-Jørgensen and Dietz 1995, Burns and Castellini 1998, Folkow and Blix 1999, Lagerquist et al. 2000, Frost et al. 2001, Loughlin et al. 2003, Laidre et al. 2003). Such instruments can relate behavior to spatial location and area use and consequently show great promise for habitat selection studies in the marine environment (Barber et al. 2001, Boyd et al. 2002, Lea and Dubroca 2003).

Arctic cetaceans, like the narwhal (*Monodon monoceros*), integrate a large range of habitats across an annual cycle. Narwhals make an extensive annual migration in the fall from high Arctic summering grounds to lower Arctic wintering grounds, the spatial and temporal timing of which is tightly linked to the cyclical seasonal changes in Arctic waters. Narwhals return to their summering site origin after migrating north in the spring (Heide-Jørgensen et al. 2003a) having traversed over 3,000 km. In this study, SLTDRs were deployed on narwhals in high Arctic Canada and West Greenland between 1993 and 2001 and movements and diving behavior were monitored for several 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. This study develops spatial and statistical methods for analyzing SLTDR data and extends the applicability of remotely sensed movement data into resource selection studies.

METHODS

Satellite telemetry data

Narwhals were caught using nets set perpendicular to the shoreline (details described in Dietz et al. 2001). SLTDRs manufactured by Telonics (Mesa, AZ) and Seimac (Canada) were programmed and cast in epoxy by Wildlife Computers (Redmond, WA) with approximately 0.5 watt power output. Transmitters were attached to female whales 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 4 size categories: <375 cm = 1, 375-424=2, 425-474=3, $\geq$475 = 4).

Data from twenty-six narwhals were used in the analysis. Transmitter longevity, influenced by a number of factors, varied by individual and consequently individuals were not tracked for the same duration of time. Whales were tagged in 1993-1994 in Melville Bay, West Greenland (Melville Bay summering sub-population) (n=8), 1997-1999 in Tremblay Sound, Canada (Eclipse Sound summering sub-population) (n=11), and 2000 in Creswell Bay, Canada

(Somerset Island summering sub-population) (n=7). 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. Whales were assigned to both a summer and winter sub-population region. Whales from summering regions of Melville Bay and Tremblay Sound inhabited a southern wintering ground (SWG) and whales from the summering region of Creswell Bay inhabited a northern wintering ground (NWG). A single daily good quality (Location quality 1-3) Argos position was selected for each whale during the peak satellite passage (15:00 local time) and the temporal period between each daily position was approximately 24 h (SD 2 h). Distance from the coastline was calculated to examine coordination between individuals from sub-populations across years based on 24 h spaced consecutive positions and elapsed time.

All days with complete records of four 6-hour period histogram dive data were selected and used to create five 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 <400 m in a 24 h period, the average total number of dives >900 m in a 24 h period, and the average total number of dives >24 minutes in duration in a 24 h period. Two additional dive variables (not derived from binned dive data) were the percent of time spent at the surface ($\leq$8 m) and the dive rate (dive >8 m). Averages for a 24 h period were composed of the average of available 6-hour periods multiplied by 4. All dive parameters were linked with the corresponding daily geographic position for each individual. 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. Dives >900 m were examined to elucidate the frequency of benthic foraging dives. Dives >24 minutes in duration were used to examine prolonged dives indicating intensive search behavior or deep dives. Finally, daily dive rate and surface time, though not indicating depth selection, indexed the use of surface waters and frequency of departure from them.

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 southern most point of approximately 66°N. The chosen standard projection was Polar Stereographic (units meters) with a central meridian of 95°W and 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 ArcINFO 8.3. A categorical variable depth grid was also created with three depth categories: 0-500 m (shelf), 500-1,500 m (slope), 1,500- 2,300 m (deep). Sea-floor slope was calculated as integer value of the percent rise between adjacent bathymetry grid cells and classified into one of 4 categories, as follows: 0%, 1-2%, 3-4%, and ≥5% rise.

Point samples of bottom temperature (n=331) were obtained during random otter trawl surveys for Greenland halibut conducted in Baffin Bay and Davis Strait between 16 September and 15 November 1999 and 2001 aboard the research vessel *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 1482 m. A surface of continuous bottom temperature in Baffin Bay was built using a spherical ordinary kriging model. The continuous bottom temperature grid (ranging from 0.2 to 4.5^{o}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 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, depth, and bottom temperature variables in ArcINFO. The nearest straight-line distance to the mainland coastline from each daily position was calculated in km.

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, dives <400 m) were analyzed with the linear mixed effects procedure fit with maximum likelihood methods (LME) in S-PLUS Version 6.1. Dependent variables measuring non-normal counts of the number of dives >900 m or >24 minutes 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. 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. For GLMMs, the AIC value is approximate since likelihood evaluation is computationally difficult. 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. No interactions were explored. Bottom temperature, only available for positions from whales after 15 October (Day of Year: 288) 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 sampled year.

RESULTS

Numbers of dives

The average daily total number of dives <400 m met assumptions of normality due to a large daily sample size for each animal 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 quantifying this behavior from 19 individuals. Average daily dives <400 m was explained by categorical depth, distance from the coastline, size category, and sex (Table 8.1). Dives <400 m occurred (on average 149 per day (SE 31)) with approximately the same frequency on the shelf

(0-500 m) and in the deep (1500-2,300m) depth categories. Dives <400m declined with increasing distance from the coast. Dives <400 m were most commonly made by animals in size class 3 or female narwhals, categories which were likely correlated. Behavior of dives <400 m was 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 total number of 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. Dives >900 m, analyzed based on 1,281 records, were negatively correlated with focal mean depth and slightly positively correlated with focal minimum depth. This parameter increased with increasing distance from the coast (Table 8.2), corresponding to greater availability of deep depths. Dives >900 m were not found to be related to any physiological or population parameters. Whale-to-whale variation accounted for approximately 43% of the total error variance in the dives >900 m model.

Durations of dives

The average total number of dives >24 minutes in duration 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. Dives >24 minutes were 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 8.3). Prolonged dives increased with increasing focal depth and increasing distance from the coast. Prolonged dives were also more frequent on the Southern Wintering Ground. Whale-to-whale variation contributed to 53% of the total error variance in this model.

Dive Rate

The average daily dive rate 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 of positions quantifying this behavior from 22 individuals. Dive rate was highly dependent on depth, where the focal mean depth and categorical depth entered the model. An average dive rate (7.8 dives per hour, SE 1.02 for a size category 1 narwhal) was negatively related to focal mean depth. Dive rate was also dependent on size category where whales in size category 3 made 2.4 more dives per hour than whales in other size categories (Table 8.4). Dive rate behavior was correlated for an extended period, out to approximately 36 days. Whale-to-whale variation accounted for 25% of the total error variance in the model.

Surface Time

The estimates of percent of the day spent at the surface contained 1,224 records from 22 individual 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 8.5). Surfacing time had a clear seasonal component, being highest in the summer (approximately 48%) and lowest in the winter (approximately 36%) with an intercept value for migration equal to the intercept 43% (SE 4.6). There were large differences in surfacing 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 out to approximately 12 days. Whale-to-whale variation accounted for 30% of the total error variance in the model.

Distance from the coast

Whales from discrete sub-populations displayed highly 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 showed remarkable similarity in movements to the previous year. Whales from discrete sub-populations moved 100-200 km offshore within days of each other, often on the same day (Figure 8.1), with only 2 individuals deviating from this pattern across 7 years. No other behavioral variable in this study showed such coordination or similarity between individuals. The multivariate habitat model for distance from the coastline (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. There was little correlation between measurements of daily travel distance for whales, no more than 1.69 days. There was also very little whale-to-whale variation as a contribution in the model (less than 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-set to include only days after 15 October (Figure 8.2). In these models, the introduction of bottom temperature displaced bathymetry predictors one step down. The effects of increasing bottom temperature included decreasing dive rate, decreasing number of dives <400 m, decreasing number of dives >900 m and decreasing number of dives >24 minutes in duration, and increasing surface time. The spatial location of narwhal wintering grounds corresponds to a sharp temperature gradient along the slopes of the east side of Baffin Bay, where temperatures rise from 0^{o}C to 4.5^{o}C on the shelf. Whale locations were concentrated in the bottom temperature range between $0\text{-}1.5^{o}$C. Catches from trawls in Baffin Bay obtained during Greenland halibut surveys in 1999 and 2001 show highest densities occurring in bottom temperatures $<1.5^{o}$C (Figure 8.3).

DISCUSSION

This study utilized movements and dive data collected from narwhals 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 spatiotemporal variation in distribution and behavior and may integrate several habitats in their daily range (Macdonald and Rushton 2003). Additionally, behavioral patterns and narwhal choice of area use are to some extent determined by evolution, experience, and inherent site-fidelity of a sub-population. Nevertheless, the utility of a modeling approach linking geographic movements, behavior, and the environment over space and time offers a method for relating biological processes to the dynamics a population and 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, they often fail to take into account the possibility that either the environment and behavior may be autocorrelated. Temporal autocorrelation in dive behavior parameters and movement measurements is often stronger than spatial autocorrelation with a species whose behavior is strongly linked to seasonal cycles. Temporal autocorrelation was addressed in the models presented in this study by modeling it as a spatial variable in time. The temporal autocorrelation parameters in the models suggest behavior was autocorrelated anywhere from 2 days to over a month, depending on the dive parameter of interest.

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 driving 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 temperature are often used by necessity as proxys for sampling the distribution of prey resources.

Not all behavioral metrics may be closely related to the environment and accordingly may not be easily explained in habitat models. The highly synchronized movements demonstrated by whale positions and speed relative to distance from the coastline indicate sub-population movements are highly coordinated and generalizations about resource selection from a sample of tagged individuals can be extended to the population level (Figure 8.1). The insensitivity of the coastline 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.

Models for behavioral variables were universally dependent on some environmental parameter or 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 (Tables 8.2 and 8.3). The dependence of deep or prolonged dives on depth is not surprising as this behavior is most commonly observed far offshore in waters >1500 m. Dives >900 m were negatively correlated with focal mean and slightly positively correlated with focal minimum depth. This suggests that although focal mean explains most of the variance some portion can be explained by focal minimum. 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 minutes) was found on the Southern Wintering Ground following well with evidence of greater benthic predation in this region. Other behavioral metrics like dives <400 m, surfacing time, and dive rate were also dependent on physiological parameters like size categories.

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 cool and highly uniform on the west side of Baffin Bay, no higher than 1.0°C (Figure 8.2). East of the Baffin Bay abyss towards the West Greenland coast, bottom temperatures display a steep warming gradient along the slopes towards the shelf rising from 1.0 to 2.5°C between depths of 2,000 and 500 m. On the east side of the shelf bottom temperatures are much warmer than the west side, as high 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 for most of the year (Heide-Jørgensen and Laidre In Press).

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. Whale choice of areas with high gradients in bottom temperatures likely are related to two things: predictable open water where bottom temperatures begin to warm on the east side of Baffin Bay or 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 (Chapters 4 and 5). The behavioral effects of increasing bottom temperature (decreasing dive rate, decreasing number of dives to all depths and long durations, and more time at the surface) are consistent with less intensive foraging or searching behavior with warmer bottom temperatures.

Greenland halibut are widely distributed in the Northwest Atlantic and are found from Davis Strait northward into Baffin Bay. The main spawning area is believed to be located in 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 1988, Jørgensen 1997a). 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 have a sympatric distribution with the deep-water Greenland halibut resources in Baffin Bay (Dietz et al. 2001, Heide-Jørgensen et al. 2002a, Treble and Bowering 2002), show concentrated diving behaviour within the depth range of high Greenland halibut densities, and appear to impact halibut length frequencies and densities in their overwintering areas (Chapter 5, Laidre et al. 2003).

Several sources indicate Greenland halibut distribution is affected by temperature, although optimal 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 (0.5-2.0^{o}C) (Figure 8.4). Across the entire North Atlantic, Bowering and Nedreaas (2000) report high and stable catches between 0.0-5.0^{o}C, with a decline in catches in bottom temperatures above 4.0^{o}C. Trends in the North Atlantic are, however, more clear in the Northeast section, where catches peak around 1.1-2.0^{o}C beyond which the average weight per set declines. Jørgensen (1998) reports highest catches of Greenland halibut in Baffin Bay in 1987-1995 between 3-4^{o}C or at 1^{o}C. Fishing captains in Baffin Bay have recently started to target specific temperature ranges (cold regimes between 1-2^{o}C or warm regimes between 4-6^{o}C) for optimal catches (M. Treble, pers. Comm.). These reports on Greenland halibut follow 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 actually occur in higher densities than in whale wintering areas, which have been attributed to lack of predation (Chapter 5). 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 influx of North Atlantic water also influence sea ice structure and occurrence off West Greenland and create more predictable and larger amounts 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 for prey densities.

Narwhal movements and habitat choice may reflect evolutionary behavioral traits that have proved successful over centuries or larger time scales. Site fidelity may be a inheritable trait at the level of individuals. Site fidelity of a subpopulation may reflect collective experiences relative to a reliable resource that currently is no longer available. Consequently not all behavior may be explained simply using quantitative habitat models of current conditions. In the case of the narwhal, the extremely narrow habitat choice combined with an extremely narrow prey base and foraging seasonality makes for a highly adapted species that is indeed vulnerable to changes in climate or habitat availability.

Table 8.1. Linear mixed effect model parameters for the average number of dives <400 m made daily by narwhals.

Fixed Effect	Average daily total no. dives <400 m	SE	df	t-value	p-value	Model AIC
Intercept	149.199	30.804	1281	4.840	<0.0001	
Categorical Depth						14040.18
0-500 m	0					
500-1500 m	-10.341	4.278	1281	-2.417	0.016	
1500-2300 m	2.791	8.747	1281	0.319	0.750	
Distance from coast	-0.135	0.065	1281	-2.083	0.037	14037.63
Size Category						14036.31
Category 1	0					
Category 2	-16.113	26.322	19	-0.612	0.548	
Category 3	90.110	38.902	19	2.316	0.032	
Category 4	6.655	38.844	19	0.171	0.866	
Sex						14035.85
M	0					
F	36.865	23.035	19	1.600	0.126	

Table 8.2. Generalized linear mixed effect model parameters for the average number of dives >900 m each day.

Fixed Effect	Log Average daily total no. dives >900 m	SE	df	t-value	p-value	Model AIC
Intercept	-1.8280	0.383	1281	-4.769	<0.0001	
Focal Mean Depth	0.0019	0.000164	1281	11.338	<0.0001	5853.80
Focal Min Depth	-0.0007	0.000125	1281	-5.840	<0.0001	5830.71
Distance to coast	0.0053	0.0006929	1281	7.646	<0.0001	5826.21

Table 8.3. Generalized linear mixed effect model parameters for the average number of dives with duration >24 minutes each day.

Fixed Effect	Log Average daily total no. dives >24 minutes	SE	df	t-value	p-value	Model AIC
Intercept	-4.29	0.689	1184	-6.226	<0.0001	
Focal Min Depth	0.00044	0.00009	1184	4.884	<0.0001	5891.76
Distance to Coast	0.0105	0.00059	1184	17.691	<0.0001	5841.92
Wintering Ground						
NWG	0					
SWG	2.770	0.794	19	3.490	0.0024	5807.92

Table 8.4. Linear mixed effect model parameters for the average daily dive rate (dives >8 m).

Fixed Effect		SE	df	t-value	p-value	Model AIC
Intercept	7.786	1.0180	1315	7.642	<0.0001	
Focal Mean Depth	-0.0007	0.0003	1315	-2.288	0.022	5423.85
Categorical Depth	-0.131	0.1709	1315	-0.764	0.445	5421.27
Size Category						5419.11
Category 1	0					
Category 2	-0.574	1.123	22	-0.511	-.6143	
Category 3	2.453	1.328	22	1.847	0.078	
Category 4	-0.424	1.453	22	-0.292	0.773	

Table 8.5. Linear mixed effect model parameters for the average percent of time spent at the surface each day.

Fixed Effect	Average % of surface time	SE	df	t-value	p-value	Model AIC
Intercept	42.879	4.589	1224	9.343	<0.0001	
Focal Max Depth	-0.0034	0.001	1224	-3.100	0.002	9274.01
Season						9249.96
Summer	5.654	1.259	1224	4.489	<0.0001	
Winter	-6.154	1.833	1224	-3.355	0.0008	
Migration	0					
Size Category						9243.82
Category 1	0					
Category 2	5.569	4.929	22	1.129	0.2708	
Category 3	-9.356	5.798	22	-1.613	0.1209	
Category 4	8.986	6.479	22	1.387	0.1794	

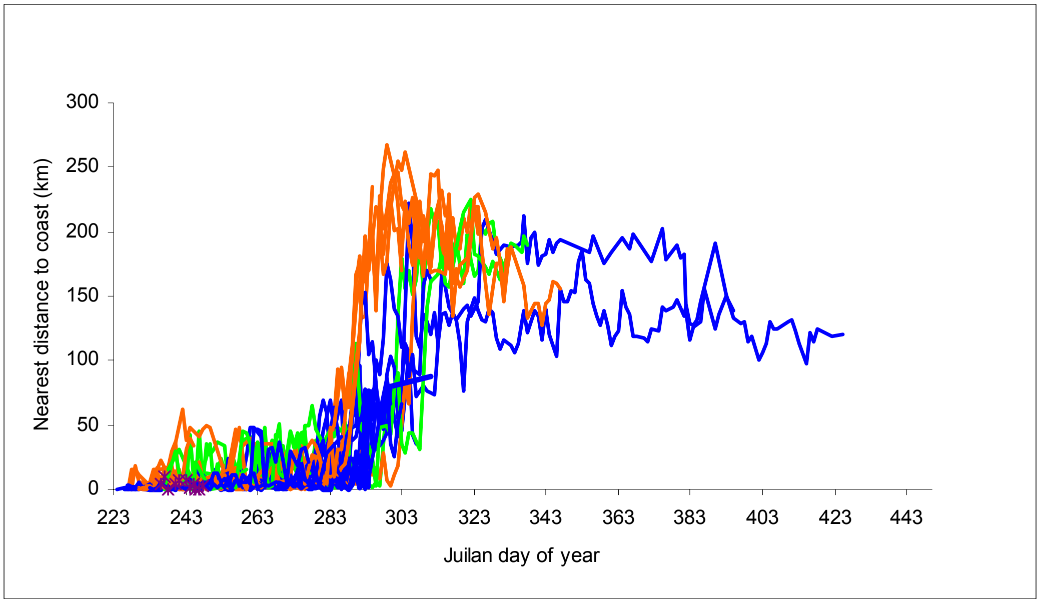


Figure 8.1. Graphs showing distance to coastline (in km) from each daily geographic position obtained from tagged whales. Sub-population and are pooled across years and shown in three colors (Blue: Tremblay Sound 1997-1999, Green: Melville Bay 1993-1994, and Orange: Creswell Bay 2000). Note the high degree of coordination between movements of individuals offshore within a sub-population and across years, with offshore movements occurring within 1-2 weeks.

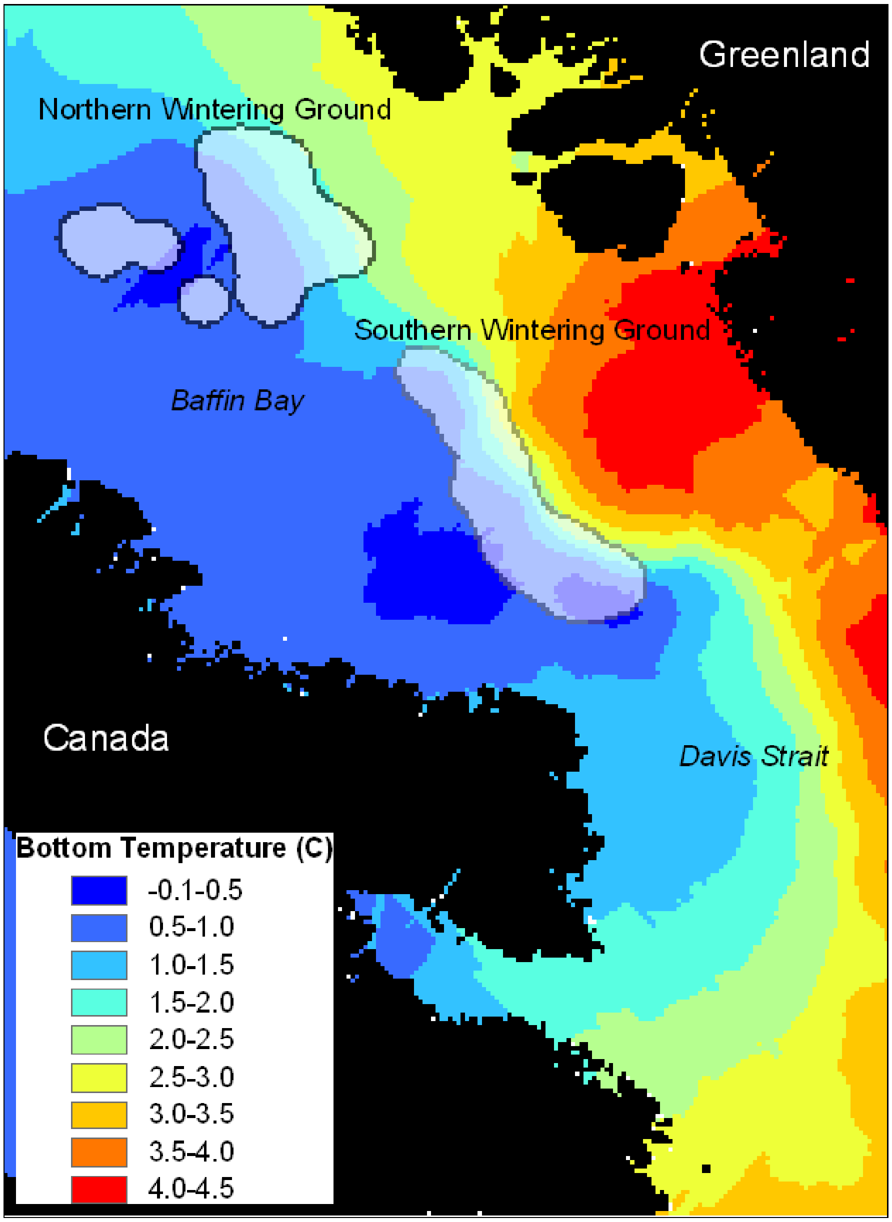


Figure 8.2. Bottom temperature contours in Baffin Bay and Davis Strait shown on a 0.5 degree C scale with location of narwhal wintering grounds.

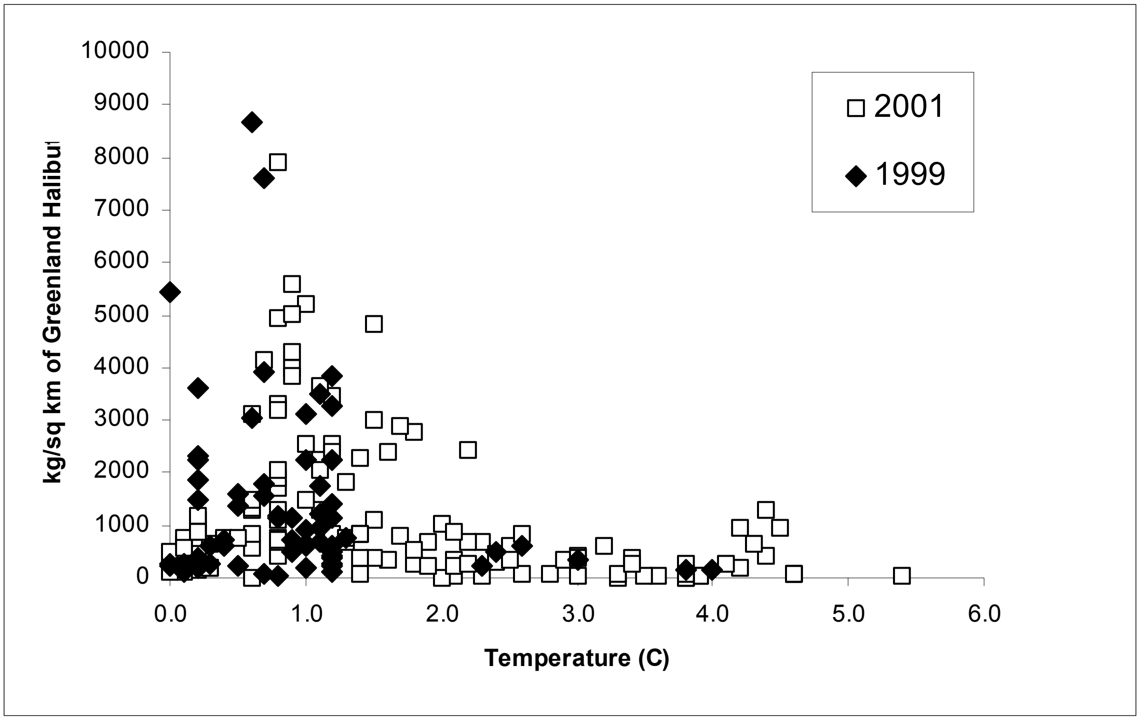


Figure 8.3. Catches (kg/km^2) of Greenland halibut in Baffin Bay in 1999 and 2001 with recorded bottom temperature at time of tow. Note catches peak between 0.5-1.0^{o}C following well with the bottom temperatures found in the narwhal wintering grounds.

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