

WINTER FEEDING INTENSITY OF NARWHALS (*MONODON MONOCEROS*)

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ABSTRACT

Stomach contents from 121 narwhals (*Monodon monoceros*) harvested in the eastern Canadian High Arctic and West Greenland were used to quantify seasonal changes in feeding activity and prey selection. Stomachs collected from summer harvests were mostly empty with little evidence of recent feeding. Stomachs collected in late fall and winter harvests had considerable amounts of undigested material with evidence of recent feeding. In summer, Arctic cod (*Arctogadus glacialis*), polar cod (*Boreogadus saida*), and *Gonatus* squid spp. constituted the narwhal diet. In fall, *Gonatus fabricii* was the only prey item observed. In late fall and winter, Greenland halibut (*Reinhardtius hippoglossoides*) and *G. fabricii* were the dominant prey items, observed in 51% and 73% of stomachs collected, respectively. Greenland halibut taken by narwhals were on average 39 cm (SD 8) and 556 g (306) and *G. fabricii* were on average 23 g (15) with mean mantle lengths of 85 mm (24). The low diversity of prey species indicates narwhals have a restricted diet across all seasons. This study presents the first information on the winter diet of the narwhal and suggests Baffin Bay and Davis Strait are heavily utilized for feeding, in contrast to limited food intake during the summer period.

Key words: narwhal, *Monodon monoceros*, diet, harvest, stomach contents, Greenland halibut, *Gonatus*.

Studies of winter feeding behavior of High Arctic cetaceans are scarce due to limited access to samples during the dark, ice-covered season or whales' offshore and sometimes unknown wintering area preferences. Because these species are almost only accessible during ice-free periods, thus summer, available diet

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investigations are dominant from that time of year. As a result, basic assumptions about feeding intensity for Arctic cetaceans have been adopted from the patterns of more easily observed lower latitude cetaceans, generally undertaking a northward migration and feeding intensively in summer, sometimes ingesting nearly all of their annual nutritional requirements in a single season (Lockyer 1981).

Among the locations in the Arctic that provide an opportunity to collect samples of cetacean stomach contents during winter is the occurrence of approximately 3,000 narwhals (*Monodon monoceros*) in Disko Bay, West Greenland, the only predictable coastal winter aggregation of narwhals worldwide (Heide-Jørgensen and Acquarone 2002). On average 154 narwhals (SD 54, range 75–268) are taken annually between the months of December and April by local hunters (catch statistics between 1993 and 2001) (Heide-Jørgensen, unpublished data). Given that reconstructing the diet of deep-diving, offshore cetaceans is difficult and in most cases can be elucidated only through stomachs collected from stranded animals or bycatch (Santos *et al.* 1999, Santos *et al.* 2001a), the narwhal provides an unusual opportunity in that it is a High Arctic, deep-diving odontocete harvested year-round.

Narwhal movements and dive behavior follow a cyclical rhythm related to seasonal changes in Arctic ice coverage and marine production. During winter months narwhals prefer deep-water offshore areas in central Baffin Bay or northern Davis Strait. From November through April, approximately 50,000 narwhals (Innes *et al.* 2002) remain in localized areas (25,000 km²) in central Baffin Bay (Heide-Jørgensen and Dietz 1995; Dietz *et al.* 2001; Heide-Jørgensen *et al.* 2002a, 2003a). During this period, they exhibit frequent deep-diving behavior, making many dives to the bottom each day (depths >1,500 m) (Laidre *et al.* 2003). Both the deep-diving behavior and evidence in offshore areas that Greenland halibut (*Reinhardtius hippoglossoides*) biomass, densities, and length distributions are impacted by predation (Laidre *et al.* 2004a) indirectly suggest the winter period may be an important season for nutritional gain.

In this study, stomach samples were collected from narwhals harvested during summer, fall, and winter months. The primary objectives were to examine winter feeding intensity and relate it to that observed from summer feeding studies. The data presented here were used to provide a comprehensive review of the seasonal feeding ecology of narwhals in the Baffin Bay and adjacent waters and to examine winter feeding behavior with respect to established seasonal patterns for other cetaceans.

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 2–5 mo in a freezer. Stomachs were taken from summer localities in Canada in Eclipse Sound (Fig. 1) between 12 and 23 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 ($n = 5$). Narwhals were taken in open water, close to shore (<10 km) at all summer localities. Stomachs were taken in fall near Uummannaq, West Greenland between 13 and 18 November 1993 ($n = 51$) and in winter by hunters in

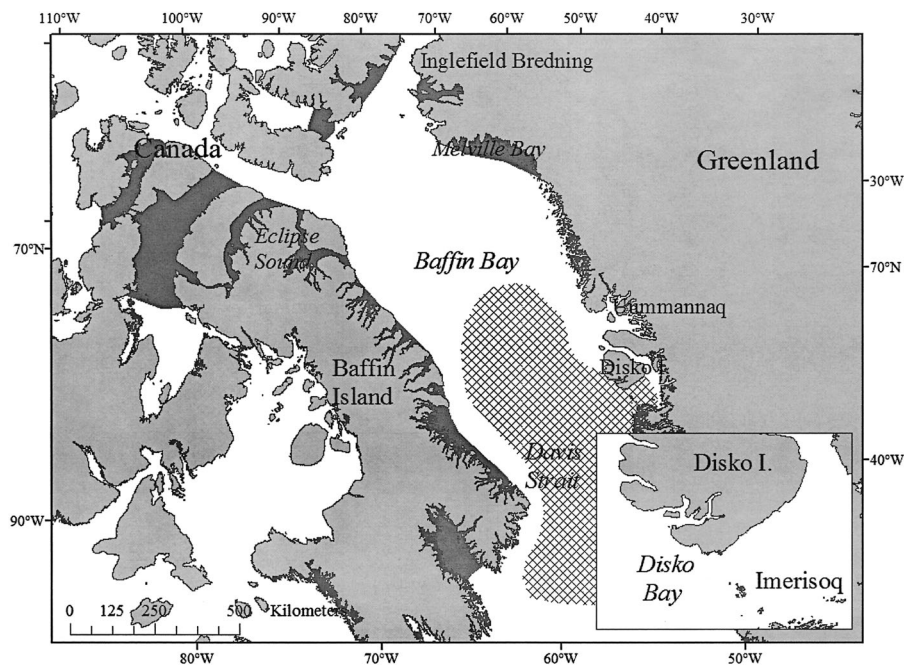


Figure 1. Map of localities mentioned in text and approximate summer (solid shading) and winter (hatched shading) distribution of narwhal subpopulations summering in the Canadian High Arctic or West Greenland and wintering in Baffin Bay, Davis Strait, or Disko Bay. Inset shows close-up of Disko Bay winter region where narwhals were harvested.

the vicinity of Disko Bay, West Greenland, between December 2002 and April 2003 ($n = 22$) and between February and March 2004 ($n = 27$). Whales were harvested in Disko Bay in 2003 over water depths up to 800 m and as far as 20 km from shore (near the island of Imerisoq), whereas whales harvested in Disko Bay in 2004 were taken < 5 km from Disko Island.

Frozen stomachs were thawed overnight for analysis and the contents were weighed. All prey items were obtained from the forestomach as rapid digestion eliminated identification of items in the main and pyloric stomachs. Fleishy 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 based on the examination of otoliths and bones from fish, crustacean skeletons, and lower beaks from cephalopods. Otoliths from polar cod (*Boreogadus siada*) and Arctic cod (*Arctogadus glacialis*) in most cases could not be distinguished and were pooled into a single category.

Stomachs with intact fish muscle, skulls, large numbers of fish bones, intact crustacean skeletons, or soft muscle attached to squid beaks were classified as having "fresh remains." Stomachs were classified based on the dominant prey species and a subsample of representative squid beaks and otoliths was collected. *In situ* otoliths were extracted and separated from those found outside skulls. Wet mass (GHL_m) in g and length (GHL_l) in mm of Greenland halibut were estimated from the otolith length (OL) by $GHL_m = 39.454 \times OL^{1.142}$ and $GHL_l = 0.2748 \times OL^{3.717}$, respectively (Härkönen 1986). Similarly, wet mass (GF_w) in g and mantle length

(GF_l) in mm of *Gonatus* was estimated from lower beak rostral length (LRL) in mm by $\ln(GF_w) = -0.655 + 3.33 \ln(LRL)$ and $GF_l = -43.3 + 42.87 (LRL)$, respectively (Clarke 1986).

RESULTS

Summer

Over half of the stomachs sampled from summer localities were completely empty and <15% contained fresh remains. Stomachs collected in Eclipse Sound, Canada, in 1999 were taken from 5 female narwhals and 3 males that ranged in standard length from 282 to 456 cm. Six of the stomachs were completely empty (two males and four females) and two contained a few (<100) upper and lower squid beaks and polar/Arctic cod otoliths, with no soft parts (Table 1). Stomachs from this area had a mean wet mass of content of <0.5 kg.

Stomachs sampled in Melville Bay ($n = 5$) in August 2002 were either completely empty or contained a few *Gonatus* squid beaks or otoliths without fresh muscle or flesh. Prey items included *Gonatus* squid spp., polar/Arctic cod, and *Pandalus* spp. (Table 1). Mean wet mass of contents was <0.5 kg. No information on size or sex of narwhals was available.

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 (four males, two females, and two juveniles of unknown sex). Average wet mass of the stomach contents was <0.5 kg. Five of the eight stomachs sampled from Inglefield Bredning were empty. Of the three that contained material (from two males and one female, >400 cm length), fresh remains were found from polar/Arctic 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 where evidence of recent feeding was observed.

Late Fall

Stomachs ($n = 51$) were collected during the annual narwhal harvest in Uummannaq, West Greenland. Two-liter subsamples of stomach contents were taken from all animals >200 cm standard length. The seventeen female narwhals and 34 males sampled during this period ranged from 205 to 490 cm in standard length. The squid *G. fabricii* constituted 100% of the diet of whales in this area (Table 1) and all stomachs had fresh remains. In addition to hundreds of squid beaks with attached muscle and eye lenses, several intact specimens of *G. fabricii* were found, suggesting recent ingestion. Out of 51 stomachs examined, only one fish bone (unidentified) was found.

Winter

Almost all stomachs (96%) taken from whales harvested in Disko Bay 2002–2004 were full of recently ingested prey items. The mean of the wet mass contents collected in December through April 2002–2003 was 5.4 kg (SD 6.5, range 0.5–30, $n = 22$). The mean of the wet mass contents collected in early February and March 2004 was 1.9 kg (SD 1.6, range 0.2–5.6, $n = 27$). No sex or age information

Table 1. Seasonal occurrence of the most common prey items in narwhal stomachs. Percent occurrence is the proportion of stomachs with a given prey item. Results from previously published studies are included for comparison. *n* is the number of narwhal stomachs examined in each study. The “% 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. Multiple years with samples from one locality were combined into a single row.

Season/habitat	Locality	Data source ^a	<i>n</i>	% stomachs with fresh	Polar/Arctic	Greenland halibut	<i>Goniatus fabricii</i>	<i>Pandalus</i>	Mean mass of wet content	
Early summer/ice edge	Pond Inlet	5	35	na	x	x	x			
		6	33	>50%	x		x			
Summer/open water	Ingfield	1	8	50%	88%	13%	38%	0%	<0.5	
	Bredning	7	35	na	75%	0%	20%		<1.5	
	Melville Bay	2	na	na	na	x	x	80%	20%	na
		1	5	0%	60%	0%				<0.5
Fall/new ice	Pond	8	3	0%	x		x	x	na	
		4	1	0%	x	0%			na	
	Inlet/Eclipse	1	8	0%	13%	0%		25%	0%	<0.5
		3	62	0%	21%					
	Sound	5	38	na	na	x	x	x		
		6	58	0%	0%	x		x		
Winter/pack ice	Uummannaq	1	51	100%	0%	0%	100%	0%	na	
	Disko Bay	1	49	96%	2%	51%	73%	20%	3.5	

^a 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 Heide-Jørgensen *et al.* 1994, ⁸ Heide-Jørgensen and Dietz (1995).

was available. The most frequent prey items were Greenland halibut and *G. fabricii*, and often only a single prey item dominated the contents of the stomach. Almost half of the stomachs were dominated by *G. fabricii* ($n = 23$) and it was the most important prey item by percentage occurrence in stomachs during winter. One quarter of the stomachs ($n = 13$) were entirely full of fresh Greenland halibut, with insignificant or no signs of *G. fabricii*. Stomachs dominated by Greenland halibut contained a greasy white film suggesting a high lipid concentration. Greenland halibut dominated the five largest and heaviest stomachs (16 to >30 kg), but was also dominant in several smaller stomachs (<10 kg). Several stomachs contained both Greenland halibut and *G. fabricii* ($n = 11$). *G. fabricii* or *Pandalus* alone were found only in small stomachs <10 kg.

Two stomachs from Disko Bay (<5% of the sample) were dominated by *Pandalus* shrimp, approximately 80–85 mm long. One stomach from April 2003 contained wolffish (*Anarhichas lupus* and *A. minor*), skate egg sacks (probably *Raja* sp.), and *G. fabricii*. Three stomachs in 2004 contained backbones from capelin (*Mallotus villosus*) <10 cm long. Rocks were found in four stomachs.

The range of sizes of *G. fabricii* suggested ingestion of both juveniles and adults and the LRL averaged 3.0 mm (SD 0.54). Based on the regression equations provided for *Gonatus* spp. in Clarke (1986) (no available species-level regressions), narwhals took an average wet mass of 23 g (SD 15) and mean mantle lengths of 85 mm (SD 24) (average across stomachs). Greenland halibut otoliths ($n = 329$) ranged in size from 3 to 10.1 mm. In 2003 the average length and mass of Greenland halibut estimated from *in situ* otoliths from five stomachs was 36 cm (SD 7) and 401 g (180). The free otoliths from the same year resulted in fish lengths and weights of 29 cm (4) and 184 g (81), respectively. In 2004 the average length and weight of Greenland halibut estimated from *in situ* otoliths from four stomachs was 46 cm (5) and 815 g (321). The free otoliths resulted in fish lengths and weights of 32 cm (7) and 296 g (241), respectively.

DISCUSSION

Biases and Shortcomings

Stomachs sampled from recently harvested animals, rather than stranded animals or bycatch, provide a less-biased picture of diet. Stomachs sampled from stranded animals, which may be unhealthy or in foreign habitat, are not 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 has not been possible to sample narwhals at their offshore wintering grounds in the heavy pack ice and instead we have used samples from a coastal wintering area as a proxy for offshore diet. It seems reasonable, based on diving behavior and residence times (Laidre *et al.* 2003), to assume similar levels of offshore feeding as those animals sampled in coastal areas.

Sources of bias such as retention time in the stomach, digestion, and secondary ingestion are generally prevalent in stomach content studies. The narwhal forestomach 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.* 2001*b*), the beaks are often trapped and accumulate in the folds of the stomach remaining undigested for a long time (Santos *et al.* 1999, Santos *et al.* 2001*b*). Fresh *Gonatus* was found only in the narwhal stomachs in fall and winter, whereas in

summer, beaks were the only evidence that narwhals had at some occasion taken *Gonatus*. *Pandalus* shrimp is the primary prey of Greenland halibut (Jørgensen 1997) and the tseli found in some of the 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. No differences were found between stomach contents of males and females when sex was available and no differences in deep-diving capabilities have been detected (Laidre *et al.* 2003). Records from the winter harvest in Disko Bay between 1990 and 1994 report 41% of the harvest was females (Heide-Jørgensen, unpublished data), indicating no large bias in the hunters selection of whales.

Seasonal Variation in Prey Items

Arctic and polar cod are important components of the summer diet of the narwhal (Vibe 1950, Finley and Gibb 1982, Bradstreet *et al.* 1986, Crawford and Jørgensen 1990, Heide-Jørgensen *et al.* 1994). The decline or disappearance in occurrence of these species (fresh remains or otoliths) between summer and winter suggests they are seasonally important. The large schools of Arctic and polar cod reported to widely occur on the summering grounds (Bradstreet *et al.* 1986, Crawford and Jørgensen 1990, Welch *et al.* 1992, Crawford and Jørgensen 1993, Welch *et al.* 1993) do not appear to be intensively utilized by narwhals.

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 not identified to species; however, they were also likely *G. fabricii*, 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 midwater depths (Kristensen 1984). Squid found in the diet of narwhals harvested in fall in Uummannaq are consistent with large schools of *G. fabricii* known to spawn in the area.

Greenland halibut was a major part of the diet of narwhals in winter and was often the only prey item identified in a completely full stomach. The species was occasionally detected in summer stomachs in Inglefield Bredning, however, never fresh or in large quantities. Greenland halibut were likely underestimated in the winter diet. Otoliths are easily digested and very fragile as exhibited by the difference in size between free and *in situ* otoliths. Narwhals also likely take Greenland halibut in intermittent intense feeding bouts, as observed by all stomachs >5 kg filled with Greenland halibut (a degree of feeding not seen with other prey items). Also, Greenland halibut are not present in high densities in close proximity (<20 km) to where the narwhals were harvested in Disko Bay in 2004. 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 may be due to the energy gained from this lipid-rich source.

Stomachs were dominated by no more than three primary prey species: polar/

Arctic cod, *G. fabricii*, and Greenland halibut. A larger number of prey species have been found in other odontocetes with a deep-diving ability (Santos *et al.* 2001a, b; Walker *et al.* 2002; MacLeod *et al.* 2003; Whitehead *et al.* 2003). The low diversity in the narwhal diet may be explained by the restriction of the annual cycle to the High Arctic ecosystem, where prey species are often found in high densities but low faunal diversities.

Seasonal Variation in Feeding Intensity

Visual observations at the ice edge suggest narwhals forage on Arctic cod and polar cod (Bradstreet *et al.* 1986, Welch *et al.* 1993, Crawford and Jørgensen 1990). After entering fjords and bays, narwhal foraging intensity is significantly reduced as evidenced by 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). In this study stomachs were largely empty during the summer period and <15% of those examined contained fresh remains. This finding is supported by previous studies examining over 244 stomachs with many completely empty or lacking fresh remains (Table 1). Summer feeding intensity in Inglefield Bredning may, however, be slightly higher than for whales summering in the Canadian high Arctic. When narwhals move out of the summering areas in the fall, stomach samples and accounts of feeding frenzies suggest they resume feeding, perhaps intensively (Finley and Gibb 1982). This study provides the first evidence that the major food intake takes place in late fall and on the wintering grounds in West Greenland and central Baffin Bay/Davis Strait, as demonstrated by the numerous full stomachs and frequency of fresh remains.

Importance of Winter Feeding for High Arctic Cetaceans

High Arctic cetaceans partition their annual cycle between coastal summering grounds and southern wintering grounds, in the most part due to the annual cycle of fast ice formation and recession. Consequently, the 3–5 mo occupancy in the summering and wintering areas is intersected by periods of migration, either in front of the forming ice or following the receding ice edge. Specifically, in the case of the winter period, whales return annually to areas with extremely dense pack ice (<5% open water) despite the high risk of ice entrapments (Heide-Jørgensen *et al.* 2002b; Siegstad and Heide-Jørgensen 1994; Laidre and Heide-Jørgensen 2005). Given observations of repetitive deep diving, habitat selection, and evidence of impacts on Greenland halibut stocks (Laidre *et al.* 2003, 2004a, b), 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 must forage on predictable prey, despite dense consolidated pack ice. Adult and juvenile survival on the northbound migration or summering grounds, as well as female condition during calving and nursing in late spring/early summer, may depend on food intake during the winter. Recently reported increases in sea-ice concentration and extent in Baffin Bay (Stern and Heide-Jørgensen 2003; Laidre and Heide-Jørgensen 2005), combined with stenophagy, or reliance on a single prey source in restricted habitat, makes a population highly vulnerable to perturbations in climate (IWC 1997).

Two other High Arctic cetaceans in Greenland 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 *et al.* 2002). During their migration out of the summering grounds, belugas increase their foraging intensity, sometimes in feeding frenzies. They are reported to arrive on the wintering grounds in coastal West Greenland and feed heavily on cod (*Gadus morhua*), redfish (*Sebastes* spp.), wolfish, and Greenland halibut, departing heavier in spring (Degerbøl and Nielsen 1930, Heide-Jørgensen and Teilmann 1994). The High Arctic mysticete, the bowhead whale (*Balaena mysticetus*), also utilizes the West Greenland region in late winter and early spring (February and March) (Eschricht and Reinhardt 1861). Bowhead whales arrive from offshore areas where primary and secondary production and feeding opportunities are less available. In West Greenland they take advantage of the rich abundance of zooplankton before departing north for less productive Canadian waters in late May (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 production, on which the high Arctic cetaceans depend. 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 2004).

General Cetacean Feeding Patterns

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), harbor porpoises (*Phocoena phocoena*) (Teilmann 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 (*Pagophilus 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 in summer and fall, 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 feeding during winter and those feeding 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 that winter out of northern latitudes in both the northern and southern hemispheres (Lockyer and Brown 1981). These populations 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. The intense winter feeding period is likely an adaptation to reduced productivity in the High Arctic summering areas after the spring production bloom, and perhaps a behavioral trait to avoid competition with lower-latitude summer feeding species. On a long time scale, the periods of glaciation have shaped the overall migration patterns of High Arctic cetaceans. However at smaller time scales, the annual formation and recession of sea ice undoubtedly governs both the ecosystem production and the whales' access to prey.

ACKNOWLEDGMENTS

Many hunters in Inglefield Bredning, Qeqertarsuaq (Disko Bay), and Melville Bay assisted with the collection and preservation of narwhal stomachs. Without their interest and dedication this work would not have been possible. Pia Barner Neve collected stomach contents from whales near Uummaannaq. Bente Jensen Graae of Arktisk Station kindly facilitated the collection of samples in Qeqertarsuaq and provided storage space and lab facilities. Bill Walker generously provided expertise in *Gonatus* identification and measurements. Support for K.L. was provided by the National Marine Mammal Laboratory, the University of Washington, School of Aquatic and Fishery Sciences, and the Washington Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, Biological Resources Division. Pierre Richard, Jack Orr, and Rune Dietz assisted in the field. Thanks to Glenn VanBlaricom, Doug DeMaster, Robert Stewart, and one anonymous reviewer for comments that improved the manuscript. This study was funded by the Greenland Institute of Natural Resources.

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Received: 12 September 2003

Accepted: 23 February 2004