

Deep-ocean predation by a high Arctic cetacean

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A bioenergetic model for two narwhal (*Monodon monoceros*) sub-populations was developed to quantify daily gross energy requirements and estimate the biomass of Greenland halibut (*Reinhardtius hippoglossoides*) needed to sustain the sub-populations for their 5-month stay on wintering grounds in Baffin Bay. Whales in two separate wintering grounds were estimated to require 700 tonnes (s.e. 300) and 90 tonnes (s.e. 40) of Greenland halibut per day, assuming a diet of 50% Greenland halibut. Mean densities and length distributions of Greenland halibut inside and outside of the narwhal wintering grounds were correlated with predicted whale predation levels based on diving behavior. The difference in Greenland halibut biomass between an area with high predation and a comparable area without whales, approximately 19 000 tonnes, corresponded well with the predicted biomass removed by the narwhal sub-population on a diet of 50–75% Greenland halibut.

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Introduction

Most marine mammals are carnivores that function as apex predators in marine ecosystems. Many prey species consumed by marine mammals are also likely to be important targets of commercial fisheries (Kenney *et al.*, 1995). Trophic interactions linking marine mammals and the marine food web have been an important conservation issue for decades and have involved a myriad of species (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 behind conflicts over interactions with marine predators. 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 example is the emerging deep water fishery for Greenland halibut (*Reinhardtius hippoglossoides*) in the offshore waters of Baffin Bay and Davis Strait. This fishery will operate in an area that overlaps the winter range of narwhals (*Monodon monoceros*).

Narwhals 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.*, 2003). The timing and extent of the fall narwhal migration is related 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 1). On the wintering grounds, large numbers of whales are concentrated in small and distinct regions over water depths up to 2300 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. They make significantly more deep dives and spend significantly more time at depths ≥ 800 m than the sub-population of narwhals from Somerset Island, Canada, occupying a separate and distinct wintering ground farther north (Heide-Jørgensen *et al.*, 2003). These differences in diving behavior have been proposed to indicate differences in local prey availability or

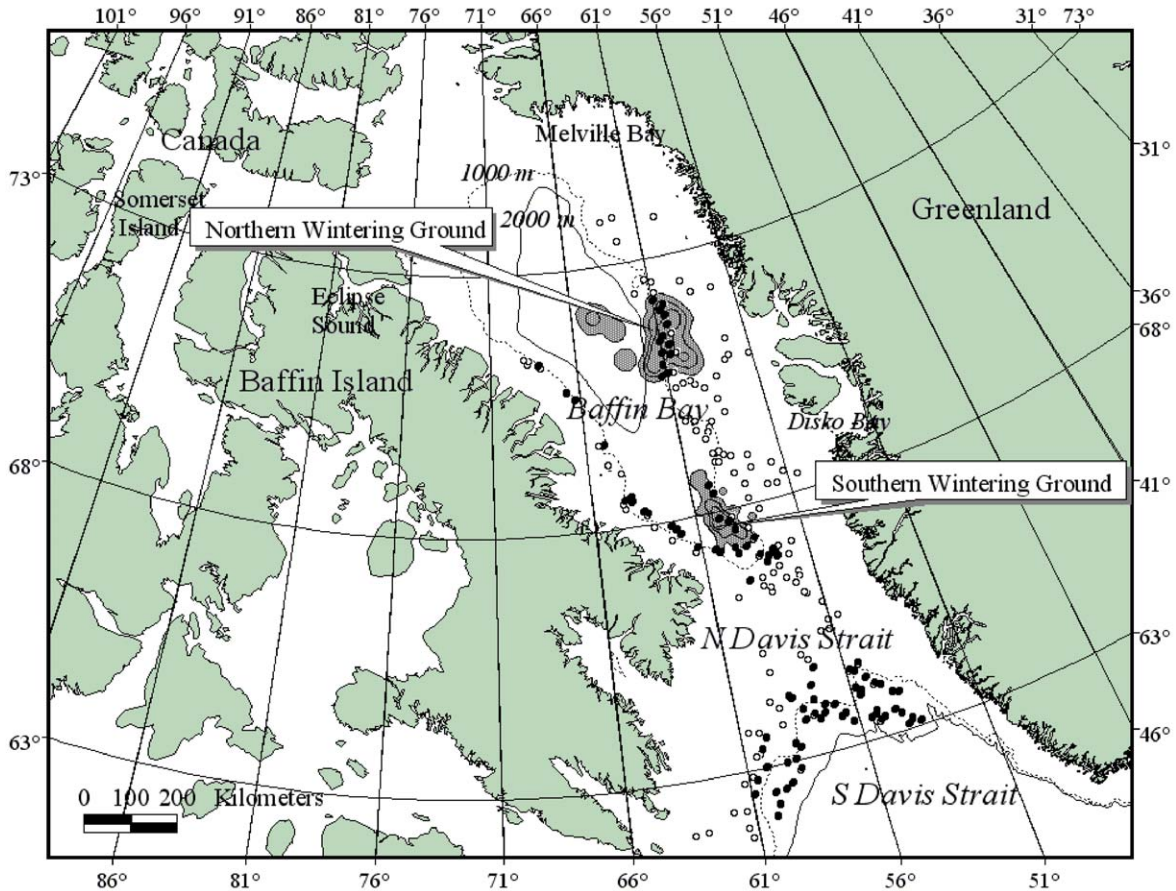


Figure 1. Map of study area, including northern and southern narwhal wintering grounds (NWG and SWG), and locations of trawl tows from the 2001 cruise used in the analysis. Tows that were ≥ 800 m and included in the analyses are shown with filled circles, all other tows (too shallow or excluded) are open circles. The 1000-m (dashed line) and 2000-m (continuous line) isobaths are shown. The area within the NWG (total 25 846 km²) between 1000 m and 2000 m was 15 679 km² and 7573 km² was greater than 2000-m depths. The area within the SWG (total 10 674 km²) between 1000 m and 1800 m was 9130 km². There was no portion of the SWG deeper than 2000 m.

foraging choice related to geographic separation of sub-populations (Laidre *et al.*, 2003).

Prey items found in stomachs of narwhals include polar cod (*Boreogadus saida*), Arctic cod (*Arctogadus glacialis*), *Gonatus* squid spp., shrimp (*Pandalus* spp.), and Greenland halibut (*Reinhardtius hippoglossoides*). Narwhal prey selection and foraging intensity have a strong seasonal component (Finley and Gibb, 1982; Laidre, 2003). In spring, narwhals take Arctic or polar cod at the sea ice edge. In summer, food consumption is at a minimum, as evidenced by hundreds of empty stomachs in diet studies (Mansfield *et al.*, 1975; Finley and Gibb, 1982; Heide-Jørgensen *et al.*, 1994; Laidre, 2003). Feeding resumes in the fall as whales move south (Finley and Gibb, 1982) and consumption peaks during winter. All stomachs examined during late fall and winter harvests ($n = 71$) were completely full and contained large amounts of fleshy undigested material, with >50% of stomachs containing only Greenland halibut (Laidre, 2003). This coupled with the regularity of deep

dives to ≥ 800 m during the 5-month period on the offshore wintering grounds is strongly consistent with offshore foraging activity on Greenland halibut (Laidre *et al.*, 2003).

Greenland halibut are widely distributed in the northwest Atlantic and are found from Davis Strait northward into Baffin Bay. Larvae from Davis Strait are carried north by currents and settle on the slopes of offshore Baffin Bay or in coastal deep water fjords of West Greenland (Riget and Boje, 1989; Jørgensen, 1997). Greenland halibut in Davis Strait and Baffin Bay most likely constitute a single stock and annual stock assessment surveys conducted in 1999–2001 estimate the biomass to be about 300 000 tonnes (Treble *et al.*, 2000, 2001; Treble and Jørgensen, 2002; Jørgensen, 2002). The species is the basis of one of the most important fisheries in Greenland, operating year-round in coastal fjords with annual catches around 20 000 tonnes (Riget and Boje, 1989; Jørgensen, 1997; Anonymous, 2002). In the 1990s, an offshore fishery developed in Davis Strait with total catches around 10 000 tonnes annually

(equal amounts taken in Canadian and Greenland waters). Within the past decade, exploitable offshore resources of Greenland halibut were discovered to the north in the deeper, central Baffin Bay (Boje and Hareide, 1993; Treble *et al.*, 2000; Treble and Jørgensen, 2002). Exploratory fishery licences were issued at depths between 800 m and 1200 m and resulted in catches between 300 tonnes and 2600 tonnes annually (Treble and Bowering, 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.*, 2002; Treble and Bowering, 2002). Additionally, they show concentrated diving behavior 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 may be subject to a large impact from narwhal predation.

A large sub-population of narwhals wintering in northern Baffin Bay exhibits more frequent and shallower 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 in the southern area and the bottom may not be as 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.

Materials and methods

Bioenergetic model

A stage and mass structured population model was developed using proportional stage classes reported by Koski and Davis (1994). Age classes of narwhals were estimated based on size and color of individuals ($n = 1230$) observed during aerial surveys in Baffin Bay: juveniles (14% of the population), immatures (19%), and adults (67%). Sex ratios were assumed to be 50:50 for juveniles and immatures, but 55% females for adults (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. Immature and mature narwhals were distinguished based on the size of sex organs at a given body weight. The median body mass for sexually mature males (1350 kg) was obtained by examining mean testis

weight vs. body mass ($n = 29$), identifying the transition point between immature and mature animals, and obtaining the median body mass at maturity. The median body mass for sexually mature females (925 kg) was obtained using the same method but by examining mean uterus weight and number of corpora marks ($n = 9$) (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 individual daily energetic needs for each stage and sex class of sub-populations of narwhals wintering in Baffin Bay. The model was used to estimate the population's daily energy requirements (kcal d^{-1}) by extrapolating using population estimates (Heide-Jørgensen *et al.*, 2002; Innes *et al.*, 2002). Basal metabolic rate (BMR in kcal d^{-1}) was calculated as:

$$\text{BMR} = 70 \times W^{0.75} \quad (1)$$

where W = the body mass in kg (Kleiber, 1975). Additional energy required for activity, growth, and reproduction was added into the model as proportions of basal metabolic rate using the simple bioenergetic model framework:

$$\text{ER} = \frac{[\text{BMR}(A + G + R)]}{\text{DE} \times \text{AE}} \quad (2)$$

where ER = energy requirement in kcal d^{-1} for an individual, 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).

Activity metabolism (A) essentially assumes that active metabolism is a constant multiple of basal metabolic rate (Lavigne, 1995; Kenney *et al.*, 1997; Winship *et al.*, 2002). Active metabolism consists of foraging behavior, movement or migration, or age- or sex-specific behavior, and has been estimated to be 2–5 times BMR in cetaceans (Lockyer, 1981; Folkow and Blix, 1992; Kenney *et al.*, 1997). A mean 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, let G range from 1.0 to 2.0 for the immature stage classes, and set G to 0 for 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 (energy for fetal metabolism and fetal growth) and lactation. Narwhals were assumed to have a calf every three years (Hay, 1984), and consequently, within a given year an “average” reproducing adult female was 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). The cost of fetal growth (450-day gestation period) was calculated using Brody’s (1945) equation for the heat increment of gestation, equal to $4400M^{1.2}$, where M is the mean birth mass (100 kg). The cost of lactation was assumed to be 3 times the combined cost of fetal growth and basal metabolism based on values reported for captive harbor porpoise (*Phocoena phocoena*) (Yasui and Gaskin, 1986). This resulted in an estimated cost of lactation of approximately twice the basal metabolic rate for a non-lactating adult, which corresponds well with that reported for captive belugas (*Delphinapterus leucas*), Atlantic bottlenose dolphins (*Tursiops truncatus*), and otariids (Kastelein *et al.*, 1994; Kastelein *et al.*, 2002; 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 (Härkönen and Heide-Jørgensen, 1991; Hammill *et al.*, 1997; Lawson *et al.*, 1997a, b; Croll and Tershy, 1998; Winship *et al.*, 2002). Values were assumed to be similar to those of 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^{-1} (1.3 kcal g^{-1}) (Lawson *et al.*, 1998). Finley and Gibb (1982) reported information on the size classes of Greenland halibut taken by narwhals, which ranged from 45 cm to 60 cm, with the largest whole specimen measuring 61 cm and having a mass of 2.4 kg. Based on catch data from 1995–2001, Greenland halibut in the 45- to 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.

Parameter uncertainty 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.*,

2002). 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, varying the proportion of Greenland halibut in the diet between 25% and 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 in September due to forming fast ice, 100% of each sub-population was assumed to occupy Baffin Bay for 5 months (150 days) of the year. Residence time 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.*, 2003). All spatial analyses were conducted in the Geographic Information System ESRI ArcGIS 8.3.

To date, three sub-populations of narwhals have been tracked into two wintering grounds in Baffin Bay (Figure 1). The 95% kernel probability area estimates were used to identify wintering regions occupied by sub-populations that have been surveyed for abundance (Heide-Jørgensen *et al.*, 2002; Heide-Jørgensen *et al.*, 2003; Figure 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 ($25\,486 \text{ km}^2$) is used by the sub-population of narwhals from Somerset Island, Canada ($n = 16$ tracked by satellite, Heide-Jørgensen *et al.*, 2003). The estimated abundance is 45 358 whales (CV 0.35) in this region, accounting for availability and perception bias (Innes *et al.*, 2002). The southern wintering ground ($10\,671 \text{ km}^2$) is occupied by two narwhal sub-populations from Melville Bay, West Greenland, and Eclipse Sound, Canada ($n = 9$ and $n = 17$ tracked by satellite, respectively), with an estimated abundance of 5348 (CV 0.43) accounting for availability and perception bias (Dietz and Heide-Jørgensen, 1995; Dietz *et al.*, 2001; Heide-Jørgensen *et al.*, 2002). 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.*, 2002; Heide-Jørgensen *et al.*, 2003).

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 their spatial distribution as well

as other potential narwhal prey. Surveys were conducted between 16 September and 15 November aboard the RV “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 knots. Mean towing time was approximately 30 min and tows as short as 15 min were included in the analysis. Trawling took place during both day and night and surveys were conducted down to 1500 m on either side of Baffin Bay and in Davis Strait (Figure 1).

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 see Jørgensen, 1998). Trawl data in Baffin Bay were examined for latitudinal or longitudinal trends in density by pooling tows into 2° latitude intervals and classified as falling on the west or east side of the Baffin Bay midline. ANOVAs were conducted to examine latitudinal trends at each 2° 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 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 other wintering narwhal aggregations likely use those areas.

Greenland halibut densities and length composition are influenced by depth (Jørgensen, 1997) and analyses of densities and length composition 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 also coincided with depths where Greenland halibut were most abundant.

Mean biomass (kg km^{-2}) and densities (fish km^{-2}) in all length classes grouped into 3-cm intervals were calculated for each of the five regions for Greenland halibut. Mean fish biomass and densities 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 biomass between regions was compared using ANOVAs and Tukey’s HSD *post hoc* analyses. The distribution of the standardized length frequency (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 $19 \times 10^8 \text{ kcal d}^{-1}$ (s.e. 7.1×10^8) (Table 1). The adult female portion of the population had the highest energy requirements, $8.1 \times 10^8 \text{ kcal d}^{-1}$ (s.e. 3.0×10^8), with adult male stage class following them at $6.7 \times 10^8 \text{ kcal d}^{-1}$ (s.e. $2.5 \times 10^8 \text{ kcal d}^{-1}$). If the daily energetic needs of the sub-population were met with a diet that comprised of 50% Greenland halibut, the sub-population would require 700 tonnes (s.e. 300) of Greenland halibut per day. The estimated biomass of Greenland halibut required by the NWG whales for the 5-month winter period ranged from 55 400 (s.e. 20 400) to 166 000 tonnes (s.e. 61 100) (Table 1) based on a diet of 25–75%

Table 1. Bioenergetic requirements for two narwhal sub-populations occupying wintering grounds in Baffin Bay (daily needs are extrapolated to a 5-month period) with predicted removal of Greenland halibut (in tonnes). The biomass removal was calculated by varying the percentage of Greenland halibut in the narwhal diet between 25% and 75%.

Wintering ground	Mean energy requirements in kcal/5 mos (s.e.)	Biomass removal (tonnes)					
		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})	55 400	26 500–105 100	110 700	53 000–210 300	166 000	79 600–315 500
SWG	3.6×10^{10} (1.6×10^{10})	6 800	2 700–14 200	13 500	5 400–28 300	20 300	8 200–42 500

Greenland halibut. Most of the variability in model estimates was a result of uncertainty in narwhal population size.

Bioenergetic predictions on the southern wintering ground

Model simulations for the sub-populations occupying the SWG (5000 whales) resulted in a population caloric requirement of 2.4×10^8 kcal d⁻¹ (s.e. 1.1×10^8) (Table 1). If the daily energetic needs of the sub-population were met with a diet that comprised of 50% Greenland halibut, the sub-population would require 90 tonnes (s.e. 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 6800 (s.e. 3000) to 20 300 (s.e. 9000) tonnes (Table 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° latitude intervals in 2001 indicated significant differences only for tows between 66°N and 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 these, 106 tows were ≥ 800 m (Table 2) and 11 of those were outside the NWG on the eastern side of Baffin Bay and excluded from the analysis. Greenland halibut were caught on 98% of tows and length classes ranged from 10 cm to 110 cm (Table 2).

The lowest density of Greenland halibut (kg km⁻²) was found in the SWG, which was about half of all other regions (Table 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 that 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

Relative length frequency distributions (Figure 2) were 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. The statistical difference was due to fish in the range of 35–55 cm missing from the two whale wintering grounds (Figure 2).

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 7100 tonnes (700 kg km⁻²) (Table 2). The biomass estimate for an area of comparable size in Baffin Bay was estimated as 26 000 tonnes (2400 kg km⁻²) (Table 2). The difference between the biomasses in these two areas was approximately 19 000 tonnes fewer fish in the SWG. This value fell within the 95% confidence intervals for a diet of 50% Greenland halibut (mean of 13 500 tonnes removed) or 75% Greenland halibut (mean of 20 300 tonnes removed) from the bioenergetic model developed for the sub-population occupying the SWG (Table 1). When the same analysis was conducted comparing the SWG densities to South Davis Strait (2200 kg km⁻²), a difference of 16 000 tonnes was achieved.

Although the density of Greenland halibut on the NWG was not significantly different from the other areas, it was

Table 2. Summary information on survey tows for Greenland halibut (GHL) and “other” fish species in Baffin Bay and Davis Strait in 2001.

Region	Number of tows	Number of GHL measured	Range of length categories for GHL (cm)	Mean density of GHL in kg km ⁻² (s.e.)	Mean density of other fish in kg km ⁻² (s.e.)
NWG	13	1 739	13–85	1 300 (200)	100 (20)
SWG	9	616	20–99	700 (300)	400 (200)
Baffin Bay	15	3 912	25–70	2 400 (600)	100 (30)
North Davis Strait	7	1 255	18–104	1 800 (400)	60 (10)
South Davis Strait	51	8 486	19–105	2 200 (200)	400 (30)
Total	95	16 008	13–105	1 700 (300)	200 (80)

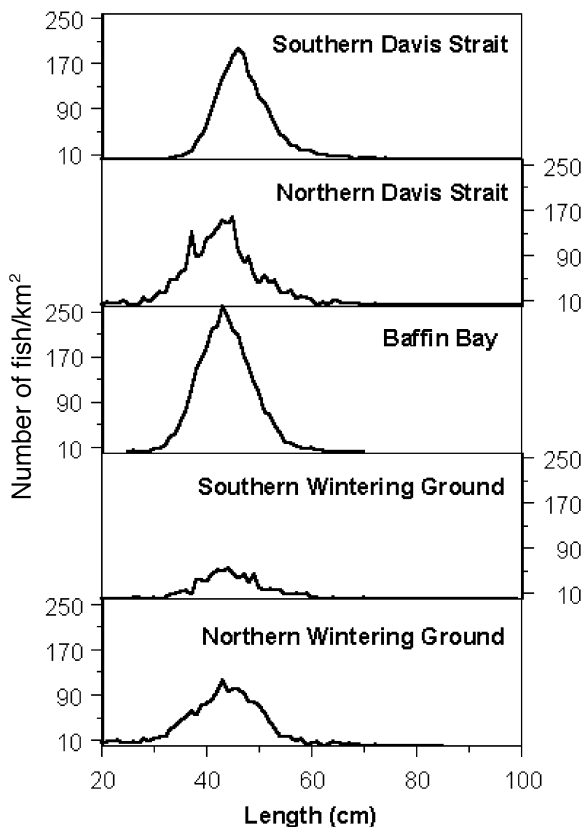


Figure 2. Distribution of the number of Greenland halibut/km² by length class in the five regions. The SWG is hypothesized to have high predation levels, NWG is hypothesized to have low predation levels, and NDS, SDS, and Baffin Bay are hypothesized to have little or no predation.

still much lower than that in the western part of Baffin Bay. The biomass of Greenland halibut on the northern wintering ground was approximately 33 500 tonnes (1300 kg km⁻²). When the biomass differences between the NWG and Baffin Bay were examined across an area comparable to the NWG (26 000 km²) (Table 2), a difference of ~29 000 tonnes was produced. The results of the bioenergetic model indicated that this sub-population would consume somewhere between 54 500 and 166 000 tonnes of Greenland halibut (Table 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 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 400 kg km⁻². The pattern of densities was also different. The highest densities of other species were found

in the SWG and the South Davis Strait. Densities were lower in Baffin Bay, the NWG, and North Davis Strait.

Approximately 4000 tonnes of other fish species exist in the SWG or an area of comparable size in South Davis Strait, with regions of comparable size in Baffin Bay or the NWG having as low as 700–1400 tonnes. Assuming 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° increments of latitude, estimates increased linearly from 66°N to 73°N, ranging from 15 fish/km² (s.e. 12) to 6500 fish/km² (s.e. 4500). Large catches did not occur below 70°N and the mean abundance increased by a factor of 5–15 at latitudes above 71°N (Figure 3). The length of polar cod ranged from 4 cm to 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 as qualitative indicators.

Discussion

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; Härkönen and Heide-Jørgensen, 1991; Murie and Lavigne, 1991; 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 the 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 (Mohn and Bowen, 1996; Boyd 2002). Although comprehensive detailed models have been built attempting to

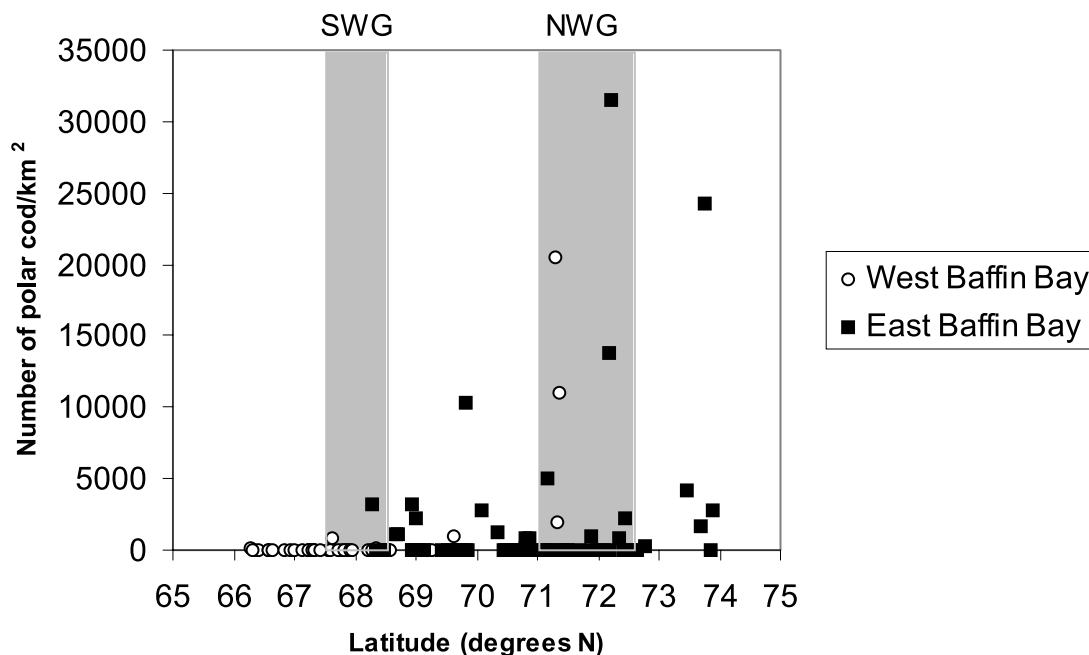


Figure 3. Abundance of polar cod in west and east Baffin Bay, 2001, shown with latitude (degrees N) of each trawl location. The NWG and SWG latitude limits are shaded. The large number of zero observations is due to the schooling behavior of the pelagic species.

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 by Welch *et al.* (1993), who estimated an 880-kg beluga would require approximately 22 kg of Arctic cod d^{-1} . In this study, an adult female narwhal (925 kg), a close Arctic relative of the beluga, required approximately 4.5×10^4 kcal d^{-1} , resulting in a maximum of 35 kg of Greenland halibut.

Large and significant differences in Greenland halibut density were observed between the SWG and other areas (Table 2, Figure 1). The lowest Greenland halibut density occurred in the SWG, which was the region with the hypothesized highest predation rates (Laidre *et al.*, 2003). 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 ≥ 800 m taken during the 1999 survey in Baffin Bay was 2000 kg km^{-2} (s.e. 370), quite similar to that observed in the same area in 2001 (mean 2400 kg km^{-2} , s.e. 590) (Table 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 that from Baffin Bay (1200 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 300 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 fish abundance estimates. 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 diets 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 as 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 (Laidre *et al.*, 2003). Note that the density of Greenland halibut in the NWG was still lower than in Baffin Bay, suggesting that 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). Laidre (2003) reported narwhals in Disko Bay, West Greenland, took Greenland halibut ranging from 9 cm to 55 cm, with a mean of 36 cm (s.e. 3). The 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 their presumed spawning area in the Davis Strait as they grow (Jørgensen, 1997). 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 increasing 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 tonnes 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.

The pattern of increasing abundance of pelagic polar cod with increasing latitude may offer insight into the observed diving behavior on the NWG. 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^{-1} , it would take a narwhal >30 min round trip to travel to 2000 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 bottom depths (1700 m), may functionally focus foraging behavior on Greenland halibut. Note that the abundance of whales on the NWG is 9 times the abundance on the SWG. It may be necessary for a larger concentration of whales to exploit several food sources to avoid direct competition. The substantial increase in the abundance of polar cod above 71°N (the NWG is located between 71°N and 72.5°N) may provide this alternative.

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 that the SWG had one of the highest densities of other fish species (together with South Davis Strait) of the five regions. These 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 midwater 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; Santos et al., 1999; Hooker et al., 2001; 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 midwater depths on the continental slopes (post-juvenile squid have been caught at depths of 200–600 m) (Kristensen, 1984; Santos et al., 2001). Estimates of density, vertical and horizontal distribution of post-juveniles in West Greenland and Baffin Bay, are relatively unknown (Piatkowski and Weiland, 1993). Surveys conducted for *Gonatus* in Baffin Bay report estimates of density of larvae at the surface or juveniles no more than 70–80 m deep (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 (Laidre, 2003). Little is known about the density or spatial distribution of *Gonatus* in Baffin Bay. Squid were observed frequently down to depths of 1400 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 that 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.

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 5000 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 (s.e. 8282) wintering in Baffin Bay based on line transect surveys conducted in late spring 1979. This estimate confirms that narwhals undoubtedly occur in large numbers and are major predators in the Baffin Bay ecosystem.

There is strong evidence that narwhal foraging intensity peaks during winter and that a large proportion of the annual energy is consumed in Baffin Bay (Laidre, 2003). 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 midwater 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 that 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 midwater 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 trade-off. 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 profitable 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.

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