

The role of the bowhead whale as a predator in West Greenland

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ABSTRACT: We examined the spatial and temporal linkage between primary production, zooplankton distribution and density, and bowhead whale (*Balaena mysticetus*) foraging behavior in Disko Bay, West Greenland using concurrent ship-based oceanographic and net sampling together with instrumentation of whales with satellite-linked transmitters and dive recorders. Estimates of bowhead whale abundance were used in a bioenergetic model to calculate the potential consumption of zooplankton during their four-month stay in Disko Bay. Between 2001 and 2006, 30 whales were instrumented with satellite transmitters providing information on daily movements and fourteen whales were instrumented with archival Time-Depth or Time-Depth-Fluorescence recorders providing detailed dive data. Simultaneous data were collected on water column structure, phytoplankton and zooplankton density, taxa, and biomass at 25 stations south of Disko Island in 2003, 2005 and 2006. After the retreat of annual winter sea ice, bowhead whales explored a limited area along the south coast of Disko Island and had high interannual site fidelity. Mean dive depths varied between 53 (± 35) to 109 (± 41) m but maximum dive depths were >400 m. Most dives targeted the bottom and dive durations >40 min were observed for several whales. Available prey for bowhead whales was dominated by calanoid copepods, with *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus* occurring at 90-100% of all stations between 0 and 50 m and contributing $78\% \pm 25$ of the total biomass. Bottom sampling for epizooplankton in 2006 resulted in unprecedented densities of *C. finmarchicus*, several orders of magnitude higher than any other depths. Bioenergetic modeling indicated the population consumes ~ 220 tons of zooplankton per day or $>21,000$ tons during the 4-month stay in Disko Bay. Although the total biomass of zooplankton in the upper 50 m of the water column theoretically could support this predation level, benthic zooplankton densities and behavioral data suggest whales target pre-ascension stage epibenthic copepods in high density patches.

INTRODUCTION

A fundamental concept in marine ecology is that the fitness of a predator depends on the spatial and temporal synchrony with the production of its prey (Cushing 1974). This is especially true in seasonal environments, where the cycle of temperature and solar radiation only allow for short production periods. The spring bloom in high Arctic marine ecosystems is characterized by relatively short efficient food chains where the large *Calanus* population grazes directly on the primary production. After the spring sea ice recession, many marine predators exploit *Calanus* for nutritional gain and build up of fat deposits. The largest zooplankton predator in this ecosystem is the bowhead whale (*Balaena mysticetus*). Recent estimates of bowhead whale abundance off the coast of West Greenland suggest over a thousand whales visit the region between February and May each year (Heide-Jørgensen et al. submitted). Several hundred whales concentrate in the Disko Bay region (Fig. 1) where they feed intensively before migrating across Baffin Bay in May and June. Satellite tracking studies of bowhead whales have documented specific fidelity to the region south of Disko Island (Heide-Jørgensen et al. 2003, Heide-Jørgensen et al. 2006). Whales have highly predictable arrival and departure dates each spring, behavior which follows observations dating back to the 1700s (Eschricht and Reinhardt 1866).

The Disko Bay population of bowhead whales is part of a larger segregated population that ranges into the Canadian high Arctic, Foxe Basin, and Baffin Bay (Heide-Jørgensen et al. 2006). Over 85% of the whales that visit Disko Bay are female and most are >14m in length (Greenland Institute of Natural Resources, unpubl data). Despite this, few calves and juvenile whales have been observed, following well with observations made during commercial whaling (Eschricht & Reinhardt 1866).

The Disko Bay is located between sub-Arctic waters of southwest Greenland and the high Arctic waters of Baffin Bay. It is influenced by both the northbound warm West Greenland current of Atlantic origin and the southbound currents of polar origin in Baffin Bay. The annual sea ice structures the springtime conditions, forming early in winter and reaching a peak coverage in March. It retreats in April and May and the bay is ice-free by June. During winter, the water column is well mixed and the lack of daylight and ice coverage prevents net growth of the phytoplankton. However in spring the growth of phytoplankton is exponential and fuels a trophic web that ultimately reaches bowhead whales. Disko Bay is relatively deep (>400 m) and sedimentation of phytoplankton begins shortly after the peak bloom phase (Pedersen et al. 2006), however frequent extreme wind mixing events reintroduce nutrients from below the pycnocline and refuel the phytoplankton in the surface layer.

Few studies have been conducted on the trophic coupling between whales and their prey given the dynamic nature of the marine environment and the difficulty in observing or quantifying concurrent whale behavior and prey availability (Croll et al. 2005, Tynan et al. 2005). In the high Arctic, long-term climate change and interannual climate variability is expected to have strong indirect effects on apex predators through trophic decoupling (Laidre et al. 2007). However, quantitative baseline understandings of the relationship between predators and their environment are required before these effects can be predicted. The primary purpose of this study was to obtain information on bowhead whale movements and diving behavior during the spring foraging period. These

data were combined with energetic demands and simultaneous oceanographic and zooplankton sampling to understand how distribution, biomass composition, and spatial variability in prey impact the springtime foraging success of the Arctic's largest zooplankton predator.

METHODS

Instrumentation of whales. Bowhead whales ($n=30$) were instrumented with satellite tags in Disko Bay, West Greenland (Fig. 1) (Telonics ST-15 and ST-16, or Wildlife Computers, Redmond, Washington SPOT1, SPOT2, and SPOT3 tags). Whales were approached in small boats and tags were pushed under the skin into the blubber layer with an 8 m long fiberglass pole (methodological details see Heide-Jørgensen et al. 2003, Heide-Jørgensen et al. 2006) or tags were deployed with an air gun (modified pneumatic line thrower). Tags were deployed in April and May 2001-2006 and location data were obtained from polar orbiting satellites via the ARGOS data collection system. A biopsy was taken from each animal and length was estimated visually.

Bowhead whales ($n=14$) were also instrumented with Wildlife Computers (Redmond, Washington) archival Time-Depth-Recorders (TDRs) (MK9) in April or May of 2002, 2003, and 2005 and with WetLabs (Corvallis, Oregon) FLNTUB fluorometers in April or May of 2005 and 2006. Fluorometers and TDRs were mounted on cylindrical shaped floats (~28 x 8 cm) with a VHF transmitter (Telonics, Mesa, Arizona) and a satellite tag (Wildlife Computers SPOT4) for instrument recovery. Floats were attached to whales using a flat 20 x 25 mm stainless steel anchoring system modified after traditional Inuit harpoon heads (4 mm thick). All instrument packages were deployed using the pole. While the whale was pursued, the float tags were held in a PVC housing mounted to the pole. Once the harpoon head was imbedded in the blubber of the whale, the float was released from the housing. The float was tethered to a 1.5 m long stainless steel wire with a corrosive magnesium bolt which released the float from the whale after a pre-determined period. Floats were recovered using real-time ARGOS satellite locations and a fine-scale VHF search conducted using directional antennas mounted on a 45 foot boat (r/v Porsild, Arctic Station, University of Copenhagen) or from a small dinghy. The TDR sampled pressure (depth) and temperature every second and had a total memory of 16MB and the FLNTUB sampled fluorescence, pressure (depth), turbidity, and temperature every second and had a memory of ~65,000 readings.

Location and dive data analysis. Average daily positions were calculated from good quality ARGOS data (LC-0 or better) for each whale. Area use during the residency period in Disko Bay, including all days after instrumentation to the departure from Disko Bay towards Baffin Island (defined as north of 70°N), was estimated using the 95, 75, and 50% fixed-kernel home range with least squares cross validation using the Animal Movement extension in ArcView (Hoodge & Eichenlaub 1997). All analyses were conducted with an equal area projection and the area where land overlapped home ranges was subtracted from the home range estimates.

Data from archival dive tags were downloaded for processing and analysis. Drift in the depth values on the TDRs was corrected using the software Instrument Helper v. 0.3 (Wildlife Computers) including both "Zero-Offset Correction" and "Dive Analysis" to produce summary statistics for each dive. The minimum depth to be considered a dive was set at 12 m (approximately the length of a whale) with a surface error of 2 m.

Bottom time was defined as 90% of dive depth. FLNTUB data were converted to measurement units using WetLabs ECOView software and processed using the same parameters as the TDR using Jensen software (MultiTrace Dive Analysis).

Maximum dive depth, dive duration, ascent and descent rates, and proportional time at depth were calculated for each dive for each individual from the raw data collected by the TDR. Standard statistics (ANOVA, t-tests) were used to contrast diving between individuals with a significance level of 0.05.

Zooplankton and water column sampling. During 5-7 May 2003, 25 systematically dispersed stations south of Disko Island in the bowhead whale concentration area were sampled for oceanographic properties, and zooplankton distribution biomass using a WP-2 plankton net (200 μm mesh and 29 cm radius) from r/v *Porsild* (Fig. 1). Vertical profiles of salinity, temperature, and chlorophyll *a* fluorescence were taken at all stations using a Seabird 25 CTD (CTD=Conductivity, Temperature, Depth). At each station, the plankton net was lowered to 50 m depth and vertically hauled towards the surface at a constant rate (approximately 10 ms^{-1}) while the vessel was stopped. After each tow, the net was rinsed on deck and zooplankton were transferred to plastic jars and preserved in $\sim 2\%$ buffered formaldehyde (final concentration).

Between 22 April and 1 May 2005, 9 stations west of Qeqertarsuaq were selected comprising a sub-set of the larger grid to focus on the areas with the highest densities of feeding bowhead whales. The zooplankton was sampled using a submersible pump (900 l min⁻¹, HOMA-H500, DIFRES-design) equipped with a flowmeter (Hydrobios), conical net (50 μm mesh size), and a non-filtering cod-end. Samples were collected in 4 depth-dependent strata. Sub-samples were taken using a sample-splitter, and the number of animals and their stages were recorded. The samples were immediately preserved in buffered formalin ($\sim 2\%$ final concentration). Additionally in 2005, a single standard station located one nautical mile south of Qeqertarsuaq ($69^{\circ}15' \text{N}$, $53^{\circ}33' \text{W}$) was monitored weekly between late-February and June. Both CTD casts and zooplankton were sampled once a week through winter and spring and a time series of temperature, salinity, and phytoplankton and zooplankton biomass was obtained.

In 2006, bottom samples of zooplankton were sampled in three target coastal areas based on direct observations of bowhead whale feeding. These areas were less than 1 km from shore (Sorte Sand, Laksebugten, and Fortune Bay), generally no more than 140 m in depth, and located in areas where bowheads predictably made feeding dives. The samples in 2006 were taken using a Hydrobios Multinet (300 μm mesh size) in five depth strata with the final strata lying as close to the bottom as possible. Strata were selected by dividing the water column into equal segments based on the maximum depth in the area. The net was lowered to the bottom and left for 15 min, where after it was hauled towards the surface at a constant rate (approximately 10 ms^{-1}). In addition, a single sample was taken with a WP-2 covering the whole water column. The samples were fixed and quantified as described previously.

In all years, mesozooplankton were sorted and identified to the lowest taxonomic level or developmental stage possible. Samples were split to obtain sample sizes of approximately 500 individuals. Each species or category was enumerated for each tow and prosome lengths were measured on up to 10 specimens for each given species or category. Total abundance was estimated by counting the number of each taxa within a

single aliquot and scaling up to the total number of aliquots in each tow. Abundance and length information was used to calculate biomass in each category at each station (mg C m^{-3}) based on values obtained from the literature (Thor et al. 2005). In 2005 these calculations were conducted by 50 m increments of the water column down to maximum depths of 200 m. *Calanus* species (stages CI-CV) and *Metridia longa* biomass were obtained from Hirche & Mumm (1992), *Acartia* were obtained from Berggreen et al. (1988), *Pseudocalanus* species from Klein Bretler et al. (1982), and *Microcalanus*, *Oithona* and *Oncaea* species from Sabatini & Kiørboe (1995). Carbon content of eggs was obtained from Kiørboe et al. (1985) and nauplii stages from Hygum et al. (2000). For non-copepod species, carbon biomass was estimated for Appendicularia (Uye 1982), Cirripedia (Turner et al. 2001), Euphausiacea (Pedersen et al. 2005), Gastropoda (Hansen & Ockelmann 1991), Polychaeta (Hansen 1999), Amphipoda (Hirche & Mumm 1992), Decapoda mysis (Uye 1982), and Chaetognata (Uye 1982). Rare taxa were excluded from biomass calculations yet were enumerated in general categories for 2003 (Table 2).

Spatial gradients in mean copepod (*Calanus*, *Metridia*, *Pseudocalanus*, *Oithona* spp.) biomass were explored with an Inverse Distance Weighted spatial interpolation model with a search radius ≥ 10 neighbors (ESRI ArcINFO 9 Geostatistical Analyst) in 2003 and 2005. Krigging in 2003 was conducted using all grid stations ($n=25$) between 0 and 50 m depths and total potential zooplankton biomass was examined with respect to bathymetry and focal area use of tagged whales. Krigging in the 2005 focal region was based on the 9 grid stations and one standard station between 0 and 50 m (Fig. 1). The number of stations with depths >50 m in 2005 were too low for spatial interpolation.

Bioenergetic modeling. A stage and mass structured population model was developed for bowhead whales in Disko Bay using proportional stage classes following directed and opportunistic observations of whales over a 5-year period. Age classes of bowhead whales in Disko Bay in winter and spring were modeled as 0% juveniles, 20% immatures, and 80% adults based on 6 years of field observations. Sex ratios were set at 85:15 (F:M) based on genetic biopsy studies (Greenland Institute of Natural Resources unpubl. data). A median body mass of 60,000 kg was assumed for sexually mature males and females (Reeves & Leatherwood 1985), and a median body mass for immatures was assumed to be half of that, or 30,000 kg.

A generalized bioenergetic model was developed to quantify the gross energetic requirements of the various population segments. The model was used to estimate the population's daily energy requirements (kcal d^{-1}) by extrapolating recent population abundance estimates of 250 whales (CV 0.35) for a region corresponding to the home range in Disko Bay (Heide-Jørgensen & Acquarone 2002). Basal metabolic rate (*BMR* in kcal d^{-1}) was calculated as:

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

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:

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

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) assumes that active metabolism is a constant multiple of basal metabolic rate (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 to 5 times BMR in cetaceans (Lockyer 1981, Kenney et al. 1997). A mean of 2.5 was used following Kenney et al. (1997).

Energy requirements for growth of body tissues and blubber, which decrease with increasing age until physical maturity, can be 110-300% of the maintenance energy required for adults (Innes et al. 1987). Therefore, growth in body mass or production was modeled as additional needs (varying with age) and calculated as a proportion of BMR. We 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. Bowhead whales were assumed to have a calf every three years, and consequently, within a given year an ‘average’ reproducing adult female in the model was pregnant, lactating, or resting. A composite energy requirement for pregnancy was based on the fetus was assumed to have a BMR proportional to that of an adult per kg (Yasui & Gaskin 1986) (mean mass 6,000 kg estimated as half the birth weight based on 3.5 m long fetus (Reeves & Leatherwood 1985) proportional to adult mass-length ratio). The cost of fetal growth (14 month or 420 day gestation period) was calculated using Brody’s (1945) equation for the heat increment of gestation, equal to $4400 M^{1.2}$, where M is the mean birth mass (13,000 kg). The cost of lactation was assumed to be three times the combined cost of fetal growth and basal metabolism (Yasui & Gaskin 1986). This resulted in an estimated cost of lactation of approximately twice the basal metabolic rate for a non-lactating adult (Winship et al. 2002). The costs of pregnancy and lactation were combined to create a value for R of 0.6 for the adult female portion of the bowhead population.

Digestive efficiency (DE) was assumed to be 0.9 following that for other marine mammals and assimilation efficiency (AE) for cetaceans was assumed to be 0.8 (Lockyer 1981). The energetic value of the *Calanus* dominated zooplankton was assumed to be 5 kJ g^{-1} (1.18 kcal g^{-1}) with a mean size of $1.0 \times 10^{-4} \text{ g}$ per individual copepod.

Parameter uncertainty was addressed with Monte Carlo simulations, where parameter values were randomly selected from sampling distributions that best described their uncertainty. 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. Population size was drawn from a lognormal distribution following Heide-Jørgensen and Aquarone (2002). Approximately 10,000 simulations were used to calculate a mean caloric requirement and confidence intervals for the spring feeding period. These prey demands were used to estimate the total amount of zooplankton consumed by the population.

RESULTS

Area use of satellite tagged whales

The 30 bowhead whales instrumented with satellite tags were all 12 m or greater in length. Average daily positions were obtained for individual whales tagged in April and May 2001 (n=5), 2002 (n=6), 2003 (n=3), 2005 (n=11), and 2006 (n=5). In all years, area use was focused on the southern coast of Disko Island extending offshore about 50 km (Figs. 2a-e). The bathymetry within home ranges varied widely and covered areas ranging from a steep coastal slope to trenches of 400 m depth.

In 2001, the movements of 5 tagged whales were focused along the south coast of Disko Island close to shore and the area use ranged up to 3,652 km² (95% kernel) during 4-21 May (Table 1, Fig. 2a). In 2002, the area use extended farther west to include Disko Fjord and a larger part of the coast of south Disko Island and was 4,502 km² (95% kernel) during 7-14 May (Table 1, Fig. 2b). In 2003, area use extended ~90 km south of Disko Island and the whales utilized up to 4,089 km² (95% kernel) during 10-21 May (Table 1, Fig. 2c). In 2005, whales utilized a similar region as in 2001 however slightly larger up to 6,897 km² (95% kernel) during 16 April-17 May (Fig. 2d). In 2006, the home range included some area use north of Disko Island, however, whales still concentrated along the south coast of Disko Island utilizing up to 35,028 (95% kernel) during 6 April-31 May (Table 1, Fig. 2e).

Diving behavior

Fourteen archival tags (TDRs and FLNTUBs) were deployed and retrieved on bowhead whales between 2002 and 2006 (Table 2). Tag attachment duration lasted between 1 h 45 min and 54 h 41 min, with an average attachment time of 11 h 40 min for all 14 samples. Most instruments were recovered 1-2 days after release from the whale using the ARGOS location data and VHF tracking. Some instruments were retrieved with mud on the instrument package suggesting recent bottom contact.

Intra- and inter-animal variability in diving behavior was high in all years. Mean inter-whale dive depths ranged from 53 (SD 35) to 109 m (SD 41) (Table 2). Dive depths ranged from 12 m to 487 m for individual whales, and the maximum depth reached by each individual was generally over 150 m (80% of tagged whales made at least one dive >150m). Significant differences in individual mean dive depth were detected ($F_{13,607}=4.25$, $p<0.001$). Mean dive durations ranged from 3 (SD 2) to 18 (SD 9) min, yet the maximum dive duration recorded was 48 min. Significant inter-whale differences were detected in dive duration ($F_{13,607}=18.0$, $p<0.001$). Descent rates and ascent rates between individuals ranged widely (Table 2) and were significantly different (Descent $F_{13,599}=22.1$, $p<0.0001$, Ascent $F_{13,554}=23.4$, $p<0.001$). Maximum observed ascent rates were higher than maximum observed descent rates. Dive duration ranged widely for a given maximum dive depth (Fig. 3a) and was poorly correlated. Furthermore, post-dive surface time was not significantly correlated with dive depth or dive duration for any individual (Fig. 3b, Fig. 3c.).

Surfacing intervals tended to be short when active diving was observed and over 50% of post-dive surface intervals, regardless of destination depth, were <4 min in length. Occasionally, diving activity ceased and whales spent extended periods at the surface. These periods of apparent inactivity were characterized by few dives below 12 m and ranged from 30 min to >6 hours in duration.

Dive shapes could be classified into two general types. Typical feeding dives were characterized by a rapid descent to a particular depth, fidelity to that depth (± 5 m)

during the bottom time portion of the dive, and then a rapid ascent back to the surface. These foraging dives were generally U-shaped (Fig. 4) with a large proportion of time near the bottom and often at the maximum depth in the area. The other type of dive identified resembled a deep V-shaped search dive that traversed a large portion of the water column (generally >100 m) with minimal time spent on the bottom. Often a series of search dives preceded a series of foraging dives with remarkable fidelity to a certain depth.

Zooplankton and water column sampling: 2003

Stations were evenly distributed in a grid network between 8 and 50 km off the southwestern corner of Disko Island (Fig. 1). Zooplankton samples were collected from a standardized volume of water (13 m^3) between 0-50 m, and whenever possible CTD casts were taken to 100 m. CTD data demonstrated a characteristic water column stratification for polar seas, with low saline and high temperature water masses at the surface extending (range -0.7 - 1.0°C and 33.1 - 33.5 psu) down to the pycnocline (20 m). There was no sign of deeper mixing in the water column however the deep advection of warm saline water was evident below 70 m. Surface temperature was approximately -1°C and declined to about 0.25°C at depths of 20 m before warming again.

Zooplankton taxa were pooled into categories representing both the largest proportions of biomass in the study area and the primary prey species for bowhead whales (Table 3). Across the 2003 grid network, copepods dominated the biomass, with *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus* occurring at 90-100% of all stations contributing on average 78% (SD 25) of the total biomass (interstation range 30-97%). Among the copepods, *C. finmarchicus* contributed a disproportionate amount of the biomass, outnumbering *C. glacialis*, and *C. hyperboreus* at least by a factor of 4. *Calanus* eggs and nauplii were found at all stations. Other copepod species (including *Metridia*, *Oithona*, *Pseudocalanus*, *Microcalanus* and *Acartia*) also contributed a large proportion of the total biomass (Table 3). Non-copepod species found frequently included Cirripedia, Euphausiacea, Amphipoda and Gastropoda, although these taxa were only identified in nauplii, egg, or larval stages and contributed minimally to the total biomass. Mean station biomass measures were normally distributed and ranged between 4 and 233 mgC m^{-3} . Average inter-station biomass for all zooplankton between 0-50 m was 79 mgC m^{-3} (SD 52).

Interpolated spatial gradients in biomass in 2003 were higher in the eastern and offshore part of the bay with lower biomass in the western part and at shallow depths (Fig. 5). The low biomass in the western portion of the bay (ranging from 4 - 50 mgC m^{-3}) spatially coincided with the 50% probability home range in 2003 (Fig. 2c). Biomass levels $>200 \text{ mg C m}^{-3}$ were found in areas where few satellite positions were received from whales in 2003.

Zooplankton and water column sampling: 2005

The standard station in 2005 demonstrated the temporal trend in the development of primary production in Disko Bay. Low chlorophyll *a* values were recorded in the upper 50 m of the water column until late March, after which phytoplankton biomass exponentially increased and peaked in mid-April at $14 \text{ mg Chl } a \text{ m}^{-3}$ (Fig. 6a). Copepod biomass peaked between the end of April and early May at $2,500 \text{ mgC m}^{-2}$ (Fig. 6b). The

temporal trend of the ascension of copepods to the upper 50 m was essentially linear and densities asymptotated at levels of $\sim 2,000 \text{ mg C m}^{-2}$ by June.

The additional focal area sampled in 2005 corresponded to the region used heavily by feeding whales. Biomass in 2003 and 2005 were compared for 9 stations (Figs. 5 and 7). Biomass to 50 m was lower in 2005 than in 2003 (between 1 and 16 mgC m^{-3}) however increasing trends with increasing distance from the coast were found in both years. Copepod biomass was five to fifteen times higher at depths $>150 \text{ m}$ where whales concentrated diving activity (Figs. 8 ab). This was the same region where biomass above 50 m was negatively correlated with whale occurrence in 2003 (Fig. 5).

Zooplankton and water column sampling: 2006

In 2006, 3 sites (Sorte Sand, Fortune Bay, and Laksebugten) were sampled for zooplankton concentrations from the surface to the bottom in 15 m increments and in 5 replicates (Fig. 1). At all sites, the biomass of copepods and *Pandalus* increased several orders of magnitude and significantly from the surface of the water column ($< 1 \text{ mgC m}^{-3}$) to an average biomass of 353 mgC m^{-3} in the bottom 40 m (Fig. 9). *Pandalus* dominated the samples between 30 and 75 m except in the last segment (between 75 and 115 m) where *C. finmarchicus* was several orders of magnitude higher than all other prey categories or depths (Fig. 9).

Bioenergetic model

The bioenergetic model produced a daily energy requirement of $2.67 \times 10^8 \text{ kcal d}^{-1}$ (SE 9.7×10^5) for the 250 (CV 0.35) bowhead whales in Disko Bay. The adult female portion of the population had the highest energy requirements, $1.2 \times 10^8 \text{ kcal d}^{-1}$ (SE 4.4×10^5) with adult male stage class following them at $9.8 \times 10^7 \text{ kcal d}^{-1}$ (SE $3.6 \times 10^7 \text{ kcal d}^{-1}$). Daily energetic needs of the population were met with approximately 223 tons (SE 0.8) of zooplankton. Thus, the estimated biomass of zooplankton required by the total population of bowheads over the 4 month period was 26,798 tons (SE 97), assuming energetic requirements for an individual are met every day in Disko Bay.

The mean biomass of zooplankton in the upper 50 m in May 2003 was estimated as 79 mgC m^{-3} . Using a carbon content of 40% of dry weight (Karnovsky et al. 2003), the biomass estimate of zooplankton corresponds to $2.6 \times 10^7 \text{ mg dry weight}$. An energy density of $26 \text{ kJ g dry weight}$ (Karnovsky et al. 2003) results in 0.001 kg m^{-3} of copepods in the upper 50 m of the water column, or approximately 122,770 tons of zooplankton in the 2600 km^2 sampled area. Thus, if bowheads feed only in the upper 50 m of the water column, they would (at the current population size) remove approximately 22% of the pelagic biomass in spring.

DISCUSSION

Bowhead foraging behavior

The U-shaped feeding dives observed in this study are characteristic for baleen whales exploiting patches of zooplankton (Baumgartner & Mate 2003, Baumgartner et al. 2003). The remarkable fidelity to a specific depth suggests that once high or sufficient densities of zooplankton are located, the dive duration at that depth is maximized and the same depth is repeatedly targeted. In this study, target depths were highly variable given that bowhead whale foraging occurred on the sea-bed in an area with a large gradient in

bottom depths. Whales actively foraged at 80 to 200 m, corresponding well to the bottom contours along the slope. The functional relationship between U-shaped feeding and V-shaped searching dives likely facilitates an active search for discrete layers of zooplankton before initiation of foraging dives.

In this study bowheads dove to a maximum of 487 m, and in many cases whales targeted depths of >200 m repetitively. In the Beaufort Sea, bowhead whales have been reported to make shallower dives (50 - 100 m) for calanoid copepods on the bottom (Krutzikowsky & Mate 2000). The dive of 487 m recorded during this study is the deepest dive measured for a bowhead whale.

Dive durations measured for foraging bowhead whales were surprisingly longer than that reported for other baleen whales. Dives lasted up to 48 minutes and in several cases whales repeatedly dove for 30-40 minutes at a time with <2 min post-dive surface time. Mean dive durations in this study (5-18 min) are similar to right whales (*Eubalaena glacialis*) (12 min), however maximum values are much higher than for right whales (16 min for right whales) (Baumgartner & Mate 2003). Balaenopterids fin (*Balaenoptera physalus*) and blue whales (*Balaenoptera musculus*) have shorter foraging dive durations (mean 6 to 7 min) and it has been suggested that continuous filter feeding in bowhead and right whales lowers metabolic rates and enables these species to maintain higher dive durations (Croll et al. 2001).

Krutzikowsky & Mate (2000) reported bowhead whale dive durations exceeding 60 min in the Beaufort Sea. Furthermore, bowhead whales have been reported to stay submerged for >80 minutes when harpooned (Scoresby 1820, Scammon 1874), and this species may have a diving capacity far beyond that of other baleen whales (Fig. 3a, Fig. 4).

Bowhead whales appear to have large flexibility in their use of the water column. There was no correlation between dive depth and duration and no correlation with post-dive surface interval (i.e., recovery time). This is in contrast to strong positive correlations between dive duration and dive depth for right whales that are focusing on dense patches of zooplankton (Baumgartner & Mate 2003).

Bowhead whales in Alaska feed between spring and fall in the water column and on the bottom or near-bottom on larger amphipods and euphausiids (Lowry 1993, Lowry et al. 2004). Lowry (1993) and Lowry et al. (2004) found hundreds of prey species in the stomachs of harvested bowhead whales between Point Barrow and Kaktovik and differences in the seasonal proportion of species in stomachs followed well with seasonal patterns of zooplankton abundance.

Bowhead prey items

Bowhead whales have been postulated to filter feed on zooplankton at depths just below the euphotic zone after the ascension of the secondary production. Therefore, the lack of relationship between high densities of prey in the upper 50 m of the water column and bowhead dive behavior and area use was surprising. The major portion of the spring zooplankton biomass in the upper 50 m of Disko Bay is comprised of Calanoid copepods. This was primarily *C. finmarchicus*, a North Atlantic species that successfully reproduces and recruits in polar ecosystems (Pedersen et al. 2005, Thor et al. 2005). Studies of interannual variation in the upper 50 m of the water column in Disko Bay indicate that zooplankton biomass can vary by >30% (Thor et al. 2005). This renders the predictability

of prey for bowhead whales in surface waters low. Bowhead whales occupy a seasonally dynamic environment with brief optimal foraging conditions. Thus maintaining a foraging strategy that targets the densest and most predictable prey concentrations (i.e. near seabed zooplankton) offers insurance against interannual fluctuations in prey abundance at the surface. Bowheads ingest about ten times as much phytoplankton as copepods while foraging (750 mg C m^{-3} of phytoplankton vs. 79 mg C m^{-3} of *Calanus*), however the extent of the importance of diatoms in the diet of bowhead whale is unknown.

Bowhead energetics

Uncertainties in metabolic rates, feeding time for baleen whales, and energetic densities of zooplankton (Costa et al. 2006) inhibit the ability to accurately model caloric needs. Several unknown and estimated parameters make bioenergetic considerations for large baleen whales simply a ballpark guess.

Bowheads seasonally migrate between localized Arctic hot spots with high densities of zooplankton. Studies of the movements of bowhead whales from satellite telemetry show intense and localized use of a single site for 3-6 weeks interspersed with long-distance movements ($>1,000 \text{ km}$) occurring over 1-2 weeks (Heide-Jørgensen et al. 2006). Travel speeds are too high (up to 200 km/d^{-1}) for foraging to be feasible during these long-distance movements and whales traverse offshore deep areas, regions with little to no zooplankton. Thus, it is possible that bowhead whale caloric needs are not met on a daily basis, yet are obtained during intense foraging periods with little to no feeding between sites. Their large body size likely acts as a buffer from the variability in pelagic productivity and allows the species to move long distances over long periods of time between regions of patchy and ephemeral productivity.

Technically, the densities of zooplankton in Disko Bay above 50 m are sufficient to support the energetic demands of the population. However the question rests on the amount of water that needs to be filtered to meet these caloric needs and if zooplankton densities are even sufficiently high enough to warrant filter feeding by bowheads. Given the bioenergetic estimates, bowheads would need to filter more than 200 million cubic meters of water per day, or 22% of the total volume of water between 0-50 m in their home range in 4 months. Densities of copepods rapidly increase with depth, especially below 150 m, and copepod densities are orders of magnitude higher near or on the bottom. The dive data indicate bowhead whales make deep dives following the highly complex bottom contours of Disko Bay, in areas where epibenthic densities of copepods are dramatically greater (Fig. 8ab and 9). Given the requirement to strain enormous quantities of water, large whales likely have evolved to exploit their zooplankton prey in regions with high density aggregations (see Croll et al. 2005, Baumgartner & Mate 2003). Little is known about the fine-scale spatial variability of these patches or how much time bowhead whales must spend searching for them.

Affinity to the southern coast of Disko Island has been reported for hundreds of years (Eschricht & Reinhardt 1866). It is likely this particular area affords feeding opportunities that are unparalleled due to physical patterns in water temperatures, upwelling, currents or high densities of lipid rich Arctic zooplankton species (Lee et al. 2006). Eschricht & Reinhardt (1866) report on departure dates of bowhead whales in Disko Bay between 1780 and 1837 with a mean date for the last sighting of whales of 1 June (range April 26 to June 25). Bowhead whale in this study departed between 10 and

21 May, precisely following observations from the past two centuries. Bowhead whales depart from Disko Bay before the ascension and peak densities of copepods in the water column (Fig. 6b), also noted for whales in the Bering Sea (Lowry 1993).

Bowhead whales in West Greenland focus foraging effort on benthic zooplankton in coastal zones, the spatial distribution of which likely results from a combination of coastal upwelling and complex bottom topography funneling or channeling prey. The steep shelf off the coast of Disko Island (0-400 m across 4 km) makes a large range of complex and deep depths available to whales over a small horizontal area and Disko Bay is known as one of the most productive areas in West Greenland (Heide-Jørgensen and Laidre 2004).

In this study, the combination of observations of bowhead whale foraging behavior collected by satellite and archival telemetry combined with intensive and localized *in situ* sampling of ocean conditions provided a tool for merging the dynamic and complex relationships between prey availability and feeding patterns. Few other methodological approaches can be used to obtain such information about the foraging ecology of a large pelagic predator given the 3-dimensional spatial and temporal scales over which the mechanisms of physical forcing, production patterns, and prey aggregation occur. The seasonally dependable dense aggregations of zooplankton in specific localities around the Arctic likely play an important role in the recovery of the eastern Arctic bowhead whale population.

Recent studies from a variety of ecosystems demonstrate that climate change can decouple species from favorable food conditions (Post et al. 2001, Thomas et al. 2001, Winder & Schindler 2004). Given the considerable abrupt reductions in seasonal Arctic sea ice extent (Holland et al. 2006), the projected rates of ice loss through the 21st century (Serreze et al. 2007), and the close coupling between sea ice and the dynamics of phytoplankton and zooplankton (Heide-Jørgensen et al. 2007), it is likely the springtime foraging conditions encountered by bowhead whales in Disko Bay will be altered. Biotic factors like competition and predation become more important at higher levels of the food chain, thus long-term studies of the ecosystem, including physical and multiple trophic levels, are required to develop a holistic understanding of how climate change will impact bowhead whales.

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LITERATURE CITED

- Baumgartner MF, Mate BR (2003) Summertime foraging ecology of North Atlantic right whales. *Mar Ecol Prog Ser* 264:123-135
- Baumgartner MF, Cole TVN, Campbell RG, Teegarden GJ, Durbin EG (2003) Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales. *Mar Ecol Prog Ser* 264:155-166
- Berggreen U, Hansen B, Kiørboe T (1988) Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. *Mar Biol* 99:341-352
- Brody PF (1945) Bioenergetic growth, with special reference to the efficiency complex in domestic animals. Hafner Publishing Company, NY. 1023 pp
- Costa AD, Durbin EG, Mayo CA (2006) Variability in the nutritional value of the major copepods in Cape Cod Bay (Massachusetts, USA) with implications for right whales. *Mar Ecol* 27: 109-116
- Croll DA, Acevedo-Gutiérrez A, Tershy BR, Urbán-Ramírez J (2001) The diving behavior of blue and fin whales: is dive duration shorter than expected based on oxygen stores? *Comp Biochem Physiol A* 129:797-809
- Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling system. *Mar Ecol Prog Ser* 289:117-130
- Cushing, DH (1974) Sea fisheries research. John Wiley and Sons, New York, New York, USA
- Eschricht DF, Reinhardt J (1866) Om Nordhvalen (*Balaena mysticetus* L.) navnlig med Hensyn til dens Udbredning i Fortiden og Nutiden og til dens ydre og indre Saerkjender. K. Danske Videnskabernes Selskabs Skrifter. Series 5, naturvidenskabelig og matematisk Afdeling 5: 433-590
- Hansen B (1999) Cohort growth of planktotrophic polychaete larvae – are they food limited? *Mar Ecol Prog Ser* 178:109-119
- Hansen B, Ockelmann KW (1991) Feeding behavior in the opisthobranch *Philine aperta*: I. Growth and functional response at different developmental stages. *Mar Bio* 111:255-261
- Heide-Jørgensen, MP, Acquarone M (2002) Size and trends of the bowhead, beluga and narwhal stocks wintering off West Greenland. *Sci Publ of the North Atlantic Marine Mammal Commission* Vol. 4:191-210

- Heide-Jørgensen MP and Laidre KL (2004) Declining open water refugia for top predators in Baffin Bay and adjacent waters. *Ambio* 33(8): 488-495
- Heide-Jørgensen MP, Laidre KL, Wiig O, Jensen MV, Dueck L, Maiers L, Schmidt HC, Hobbs RC (2003) From Greenland to Canada in two weeks: Movements of bowhead whales, *Balaena mysticetus*, in Baffin Bay. *Arctic* 56(1): 21-31
- Heide-Jørgensen MP, Laidre KL, Jensen MV, Dueck L, Postma LD (2006) Dissolving stock discreteness with satellite tracking: Bowhead whales in Baffin Bay. *Mar Mamm Sci* 22:34-45
- Heide-Jørgensen, MP, Laidre KL, Logsdon ML, and Nielsen TG (2007) Springtime coupling between phytoplankton, sea ice and sea temperature in Disko Bay, West Greenland. *Progress in Oceanography*: In Press
- Hirche H J, Mumm N (1992) Distribution of dominant copepods in the Nansen Basin, Arctic Ocean, in summer. *Deep Sea Res.* 39 (suppl. 2): 485-505
- Holland MM, Bitz CM, Tremblay B (2006) Future abrupt reductions in the summer Arctic sea ice. *Geophysical Research Letters* 33, L23503 doi:10.1029/2006GL028024
- Hooker SK, Whitehead H, Gowans S (2002) Ecosystem consideration in conservation planning: energy demand of foraging bottlenose whales (*Hyperoodon ampullatus*) in a marine protected area. *Biological Conservation* 104:51-58
- Hoodge PN, Eichenlaub B (1997) Animal movement extension to Arcview. ver. 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK, USA
- Hygum BH, Rey C, Hansen BW (2000) Growth and development rates of *Calanus finmarchicus* nauplii during a diatom spring bloom. *Mar Biol* 136:1075-1085
- Innes S, Lavigne DM, Earle WM, Kovacs KM (1987) Feeding rates of seals and whales. *J of Animal Ecol* 56:115-130
- Karnovsky NJ, Kwaśniewski S, Węślaswski JM, Walkusz W, Beszczyńska-Möller A (2003) Foraging behavior of little auks in a heterogeneous environment. *Mar Ecol Prog Ser* 253:289-303
- Kjørboe T, Møhlenberg F, Hamburger K (1985) Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. *Mar Ecol Prog Ser* 26:85-97
- Klein Bretler WCM, Fransz HG, Gonzalez SR (1982) Growth and development of four calanoid copepod species under experimental and natural conditions. *Neth J Sea Res* 16: 195-207

- Kleiber M (1975) *The fire of life: an introduction to animal energetics*. Robert E. Krieger Publishing Co., Inc. Huntington, NY. 454 pp
- Kenney RD, Scott GS, Thompson TJ, Winn HE (1997) Estimates of prey consumption and trophic impacts of cetaceans in the USA Northeast Continental Shelf ecosystem. *J of Northwest Atlantic Fish Sci* 22:155-171
- Krutzikowsky GK, Mate BR (2000) Dive and surfacing characteristics of bowhead whales (*Balaena mysticetus*) in the Beaufort and Chukchi seas. *Can J of Zool* 78:1182-1198
- Laidre KL, Stirling I, Lowry L, Wiig Ø, Heide-Jørgensen MP, and Ferguson S (2007) Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. *Ecological Applications*: In Press
- Lee, RF, Hagen W, Kattner G (2006) Lipid storage in marine zooplankton. *Mar Ecol Prog Ser* 307: 273-306
- Lowry LF (1993) Foods and Feeding Ecology. *In* The bowhead whale. *Edited by* J. J. Burns, J. J. Montague, and C. J. Cowles. Society for Marine Mammalogy, Special Publication No. 2. Lawrence, Kansas: Allen Press. pp 201-283
- Lowry LF, Sheffield G, George JC (2004) Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents analyses. *J of Cet Res and Manag* 6(3):215-223
- Lockyer C (1981) Growth and energy budgets of large baleen whales from the Southern Hemisphere. *In*: *Mammals in the Sea, Vol. III, General Papers and Large Cetaceans*, FAO, Rome, p. 379-487
- Pedersen SA, Ribergaard MH, Simonsen CS (2005) Micro- and mesozooplankton in Southwest Greenland waters in relation to environmental factors. *J of Mar Sys* 56:85-112
- Pedersen TJ, Nielsen TG, Michel C, Møller EF, Tiselius P, Thor P, Olesen M, Selander E, Gooding S (2006) Sedimentation following the spring bloom in Disko Bay West Greenland, with special emphasis on the role of copepods. *Mar Ecol Prog Ser*. 314: 239-255
- Post E, Forchhammer MC, Stenseth NC et al. (2001) The timing of life-history events in a changing climate. *Proceedings of the Royal Society of London Series B – Biological Science* 268: 15-23
- Reeves RR, Leatherwood S (1985) Bowhead whale, *Balaena mysticetus* Linnaeus 1758. Pages 305-344. *In* *Handbook of Marine Mammals, Volume 3: The Sirenians and Baleen whales*. S. H Ridgeway and Sir R. Harrison, eds. Academic Press, London. 362 pp

- Sabatini M, Kiørboe T (1994) Egg-Production, Growth and Development of the Cyclopoid Copepod *Oithona similis*. J Plank Res 16:1329-1351
- Scammon CM (1874) The marine mammals of the northwestern coast of North America together with an account of the American whale fishery. J. H. Carmany, San Francisco (Reprinted, paperback) 1968, Dover Publications Inc. New York
- Scoresby W Jr (1820) An account of the Arctic regions with a history and description of the northern whale-fishery. Archibald Constable, Edinburgh, Scotland. Reprinted by David and Charles, Newton Abbot, England
- Serreze MC, Holland MM, Stroeve J (2007) Perspectives on the Arctic's shrinking sea ice cover. Science 315:1533-1536
- Thomas DW, Blondel J, Perret P et al. (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291: 2598-2600
- Thor P, Nielsen TG, Tiselius P, Juul-Pedersen T, Michel C, Møller EF, Dahl K, Selander E, Gooding S (2005) Post spring bloom community structure of copepods in the Disko Bay, Western Greenland J. Plank Res 27 (4): 341-356
- Turner JT, Levinsen H, Nielsen TG, Hansen BW (2001) Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. Mar Ecol Prog Ser 221: 209-219
- Tynan CT, Ainely DG, Barth JA, Cowles TJ, Pierce SD, Spear LB (2005) Cetacean distribution relative to ocean processes in the northern California Current system. Deep Sea Research II 52:145-167
- Uye S (1982) Length-weight relationships of important zooplankton from the inland sea of Japan. J. Oceanogr. Soc. Jpn. 38:149-158
- Winder M, Schindler DW (2004) Climate change uncouples trophic interactions in a lake ecosystem. Ecology 85: 56-62
- Winship AJ, Trites AW, Rosen DAS (2002) A bioenergetic model for estimating the food requirements of Steller sea lions (*Eumetopias jubatus*) in Alaska, USA. Mar Ecol Prog Ser 229:291-312
- Yasui WY, Gaskin DE (1986) Energy budget of a small cetacean, the harbour porpoise, *Phocoena phocoena* (L.). Ophelia 25:183-197

Table 1. Summary dive statistics collected from TDRs and FLNTUBs deployed on 14 bowhead whales in May 2002 - 2006 in Disko Bay, West Greenland. Tag type is Wildlife Computers Time Depth Recorder (TDR) or WetLabs Fluorometer (FLNTU). Dive depth is reported in meters, dive duration is reported in minutes, and ascent and descent rates are reported in m/s. SD in parentheses. Unknown sex (U) is due to the absence of a biopsy sample from the animal.

Whale ID	Tag type	Date tagged	Sex /Size	Deployment duration	Mean dive depth	Max dive depth	Mean dive duration	Max dive duration	Mean descent rate	Mean ascent rate
2002-01	TDR	5/5	F, 15m	2 h 20 min	87 (48)	95	9 (3)	15	0.5 (0.2)	0.5 (0.3)
2002-02	TDR	5/8	U, 18 m	10 h 12 min	57 (43)	153	14 (5)	25	0.2 (0.2)	0.2 (0.2)
2002-03	TDR	5/12	U, 18 m	12 h 48 min	70 (69)	487	9 (5)	21	0.4 (0.4)	0.5 (0.6)
2003-01	TDR	5/17	F, 12 m	7 h 50 min	54 (30)	140	5 (4)	20	0.8 (0.5)	1.0 (1.1)
2003-02	TDR	5/18	F, 15 m	8 h 46 min	90 (44)	226	9 (3)	20	0.9 (0.3)	0.8(0.5)
2005-01	TDR	4/19	M, 12 m	6 h, 50 min	72 (71)	234	11 (9)	37	0.4 (0.4)	0.4 (0.4)
2005-02	TDR	4/22	M, 15-18 m	54 h, 41 min	73 (66)	245	18 (9)	48	0.4 (0.4)	0.3 (0.4)
2005-03	TDR	4/23	F, <12 m	21 h, 57 min	109 (41)	192	12 (5)	27	0.8 (0.5)	0.8 (0.6)
2005-04	FLNTUB	4/22	M, 15-18 m	6 h, 44 min	61 (73)	234	12 (5)	23	0.5 (0.3)	0.4 (0.2)
2005-05	FLNTUB	4/26	F, 15-18 m	8 h, 15 min	94 (124)	380	13 (8)	26	0.6 (0.4)	0.4 (0.3)
2005-06	FLNTUB	4/28	U, 15-18 m	5 h, 28 min	63 (38)	158	13 (11)	41	0.4 (0.1)	0.5 (0.1)
2005-07	FLNTUB	5/3	F, 12-15 m	13 h, 50 min	74 (34)	183	12 (5)	25	0.5 (0.2)	0.4 (0.3)
2005-08	FLNTUB	5/1	F, 12-15 m	7 h, 57 min	53 (35)	183	8 (4)	21	0.3 (0.2)	0.4 (0.2)
2006-01	FLNTUB	5/1	U, 15 m	1 h, 45 min	72 (30)	110	3 (2)	7	1.8 (0.7)	1.7 (0.4)

Table 2. Estimated kernel area use of satellite tagged bowhead whales in Disko Bay between 2001 and 2006. Area estimates are in square kilometers. See Figure 2 a-e for spatial distribution.

Year	N whales	50% Area use	75% Area use	95% Area use
2001	5	829	1,950	3,652
2002	6	751	2,318	4,502
2003	3	335	589	4,089
2005	11	684	1,650	6,897
2006	5	3,494	9,304	35,028

Table 3. Species identified on 25 stations during tows for zooplankton in the upper 50 m in Disko Bay, West Greenland, May 2003. Biomass estimates are in mgC per m⁻³ for each group where total biomass was enumerated. Other copepod category includes *Microcalanus* spp. and *Acartia* spp.

Plankton category	Included in Biomass calculations	Occurrence (% of stations) in 2003	Mean (mgC m ⁻³)	SD (mgC m ⁻³)
Copepoda				
<i>C. finmarchicus</i>	X	100	49	39
<i>C. glacialis</i>	X	90	2.8	2.3
<i>C. hyperboreus</i>	X	100	12.3	14.9
<i>Pseudocalanus</i> spp.	X	100	0.5	0.3
<i>Oithona</i> spp.	X	100	0.1	0.03
<i>Metridia longa</i>	X	50	0.3	1.1
<i>Oncaea</i> spp.	X	23	<0.01	Na
Other copepoda	X	83	<0.01	Na
Copepod eggs	X	100	<0.01	Na
Copepod nauplii	X	100	0.1	0.1
Other invertebrates				
Cirripedia	X	100	0.4	0.5
Euphausiacea	X	100	1.2	1.9
Decapoda	X	87	0.05	0.1
Amphipoda	X	100	1.5	1.6
(Hyperiidea)				
Gastropoda	X	100	<0.01	Na
Chaetognata	X	93	10.4	12.6
Polychaeta	X	93	0.04	0.1
Appendicularia		33		
Hydrozoa		93		
Echinodermata		10		
Ostracoda		50		
Ctenophora		3		
Protozoa		3		
Isopoda		13		
Arachnidae		3		
Nemertini		3		
Bivalvia		3		
Fish larvae and eggs		33	0.02	0.04

Fig 1. Map of Greenland and Disko Island, shown with locality names mentioned in the text and bathymetry. Sampling stations for CTD casts and plankton hauls taken between 5 and 17 May 2003 ($n=25$) are shown with symbols (both black and red). Symbols only in red are the stations sampled again between 22 April and 1 May 2005 ($n=9$). Stars indicate the location of bottom samples in 2006.

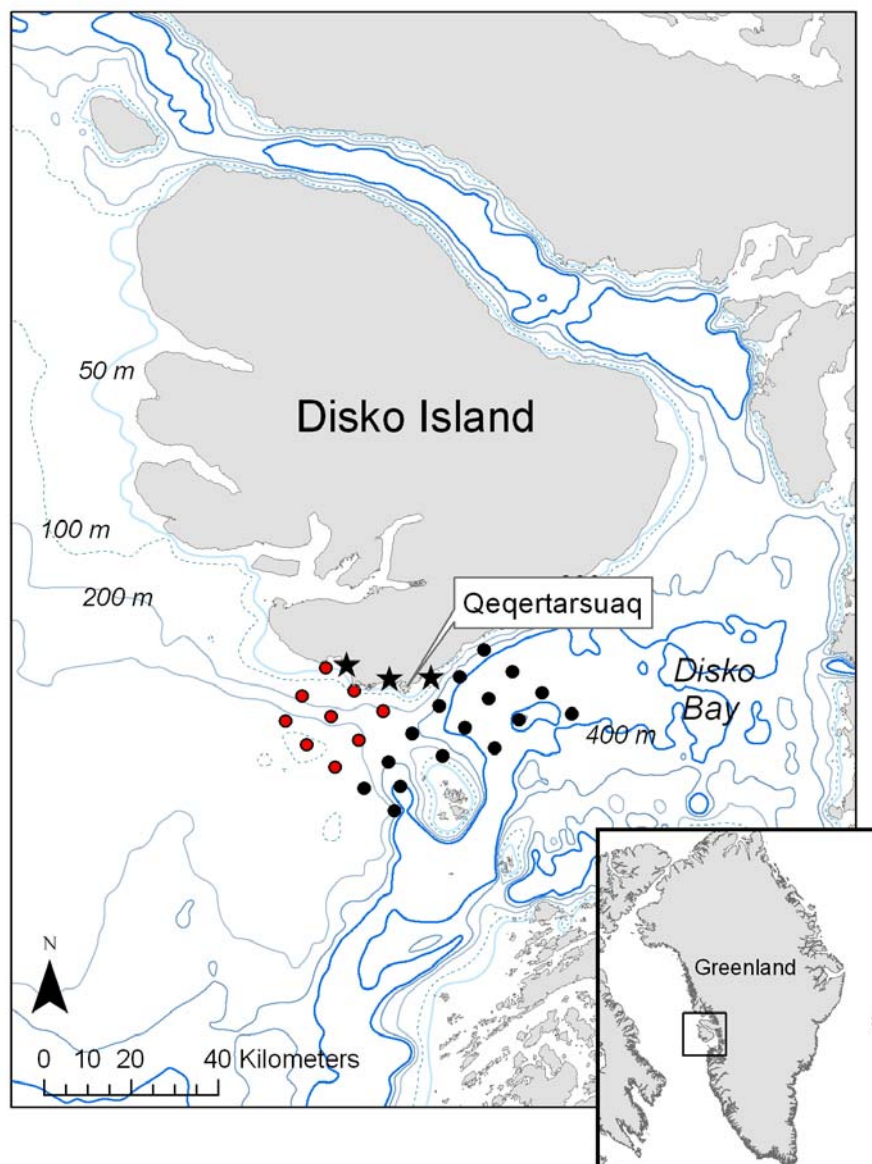


Fig 2a-e. *Balaena mysticetus* Kernel area use calculated for whales instrumented with satellite transmitters between 2001 and 2006. 95% area use is shown in light gray, 75% in medium gray, and 50% in dark gray. Data were calculated from 5 whales tagged in 2001, 6 whales in 2002, 3 whales in 2003, 11 whales in 2005, and 5 whales in 2006 using average daily positions while whales remained in Disko Bay before departing on the migration to Canada past 70°W.

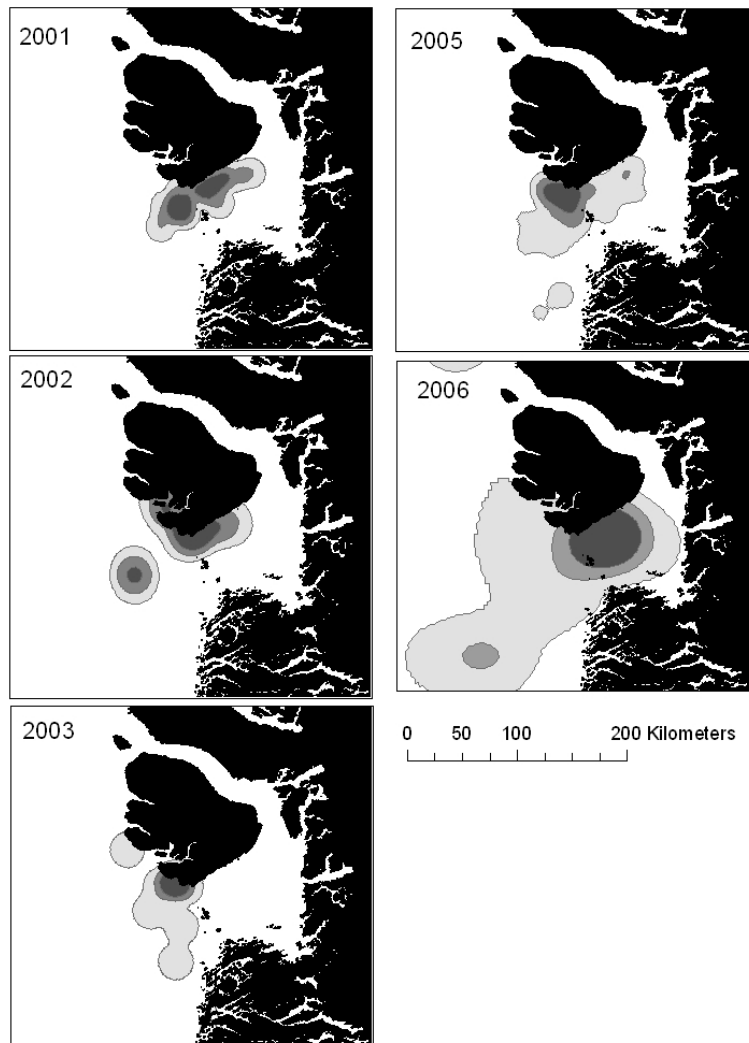


Fig 3abc. *Balaena mysticetus* Relationship between dive depth, dive duration, and post-dive surface interval for 14 bowheads tagged with TDRs in Disko Bay between 2002 and 2005 and fluorimeters between 2005 and 2006.

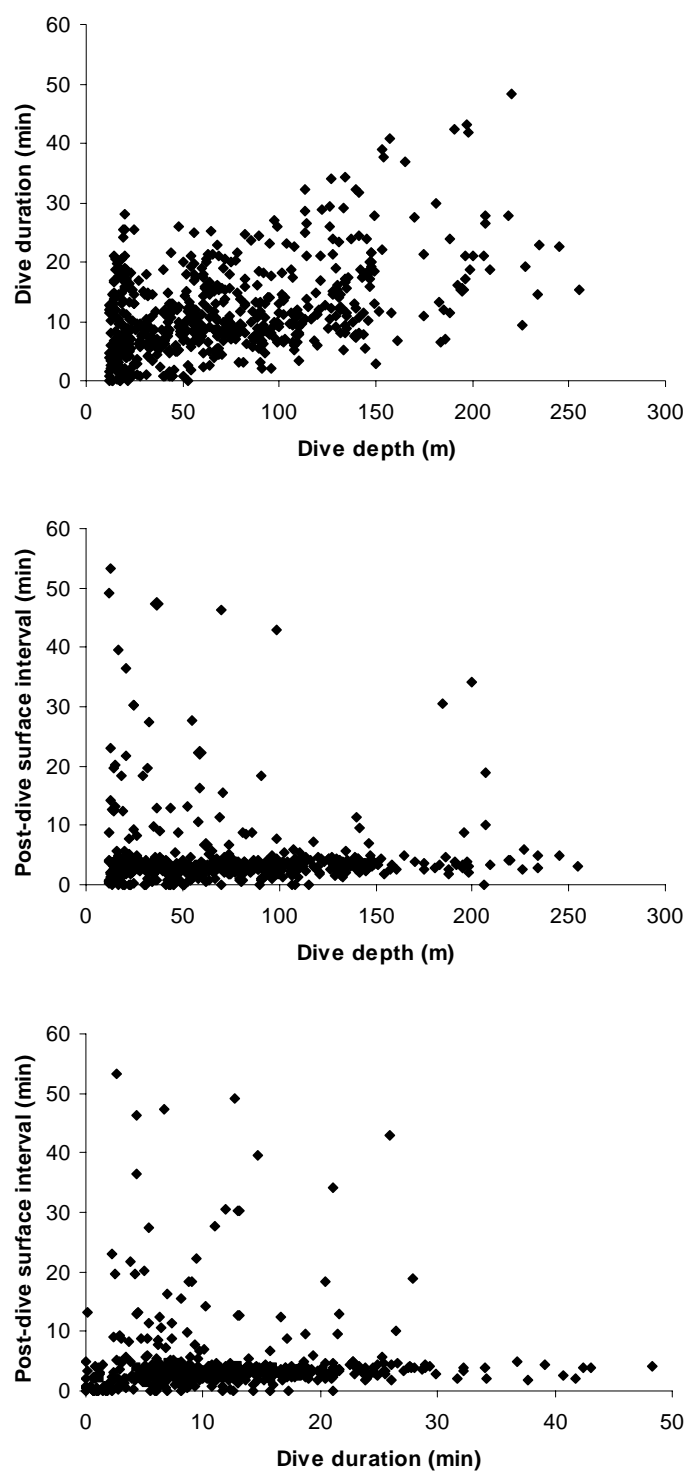


Fig 4. *Balaena mysticetus* Long-duration foraging dives of a bowhead whale (ID 2005-02). Each of the dives in the sequence lasted between 37 and 43 minutes with less than 2 minutes of post-dive surface time. Maximum potential depth in the area was 200 m.

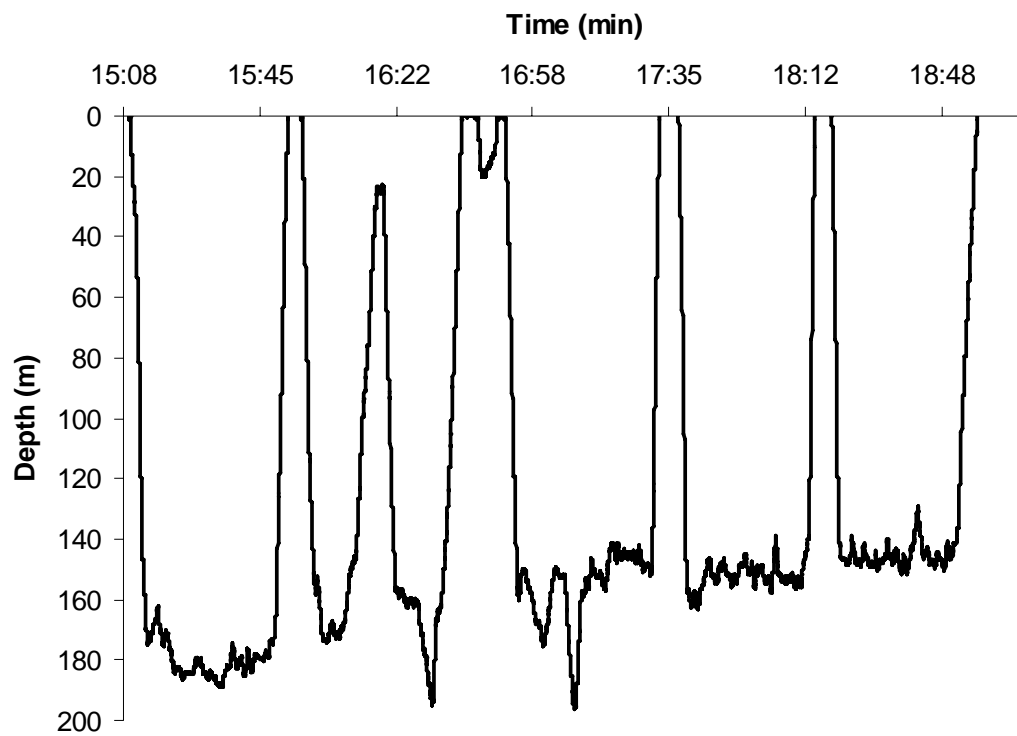


Fig 5. *Balaena mysticetus* Interpolated mean copepod biomass (per sq km) in Disko Bay in May 2003. Biomass density is shown together with bowhead kernel home range contours from May 2003 (based on satellite tagged whales, Figure 2c). Note the negative correlation between whale focal area use and biomass between 0-50 m. Station locations are indicated with dots.

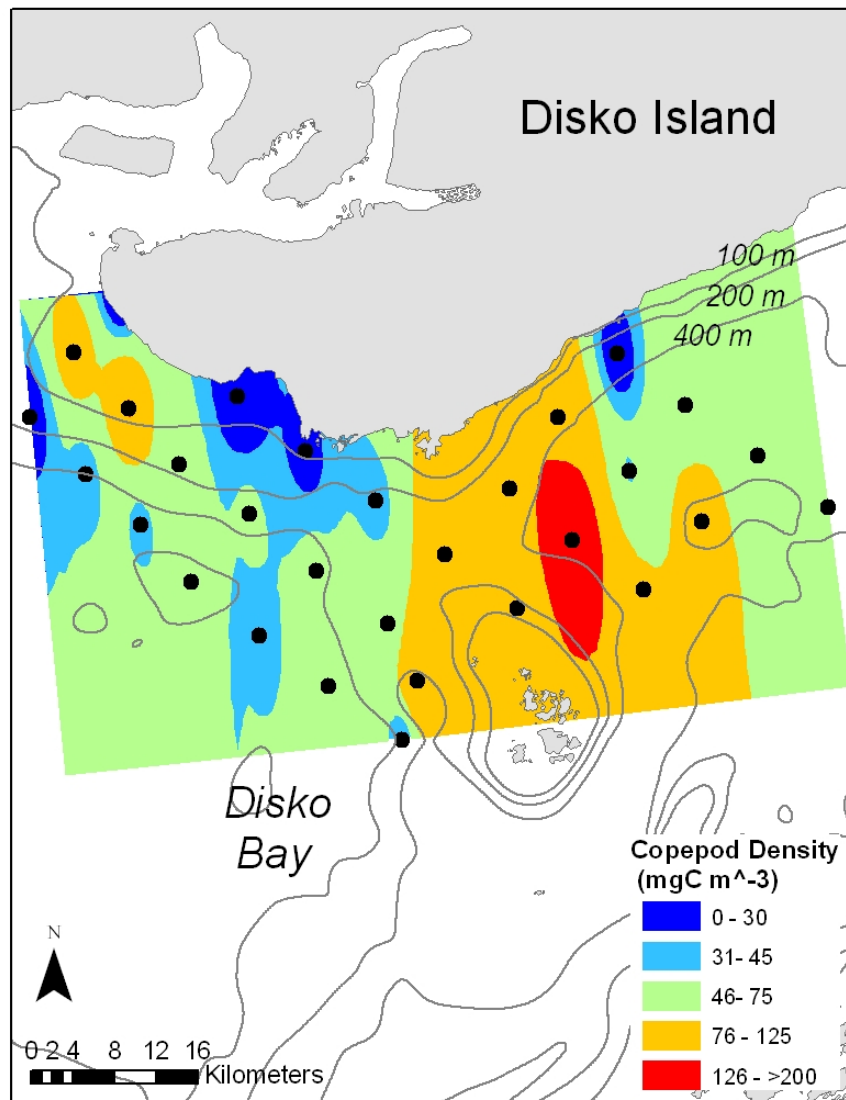


Fig 6 a. Depth distribution of phytoplankton (mgChl a m^{-3}). Points represent samples in time and the water column. Fig 6b. Integrated copepod biomass mgC m^{-2} (0-200 m). Data were collected from the single standard station monitored weekly between March and June 2005.

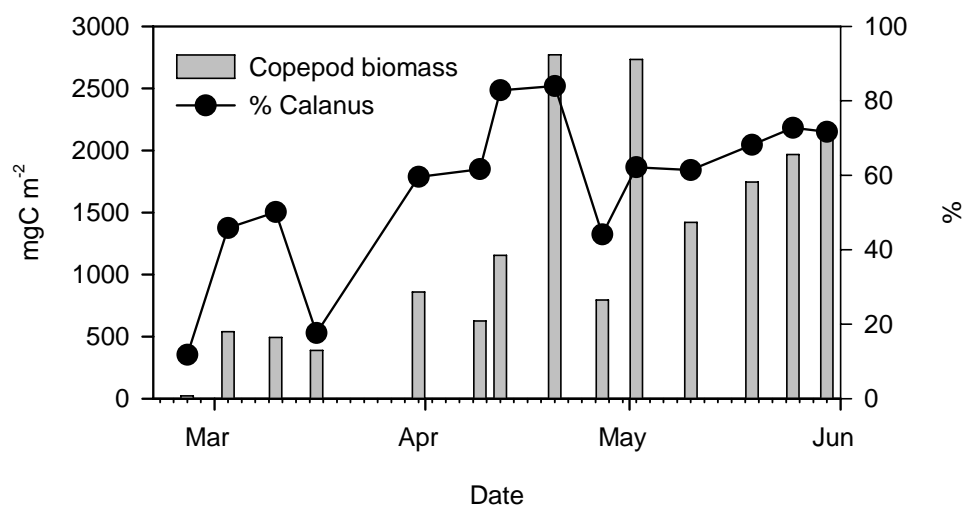
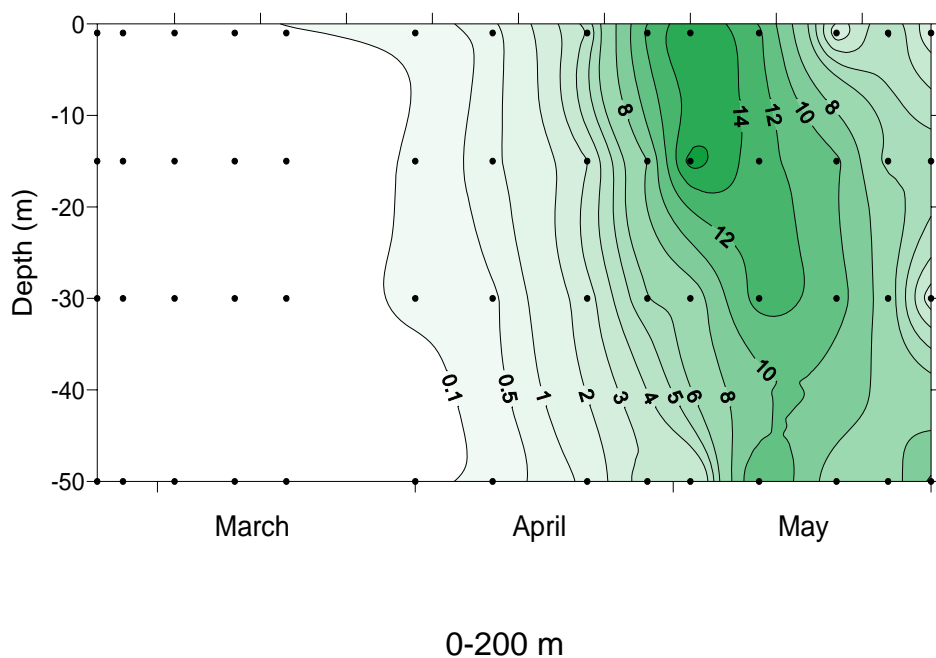


Fig 7. Spatial interpolation of copepod biomass in 2005 for 9 grid stations and 1 standard station in May between 0 and 50 m superimposed with 2005 kernel home ranges (50, 75 and 95%) from satellite tagged bowhead whales.

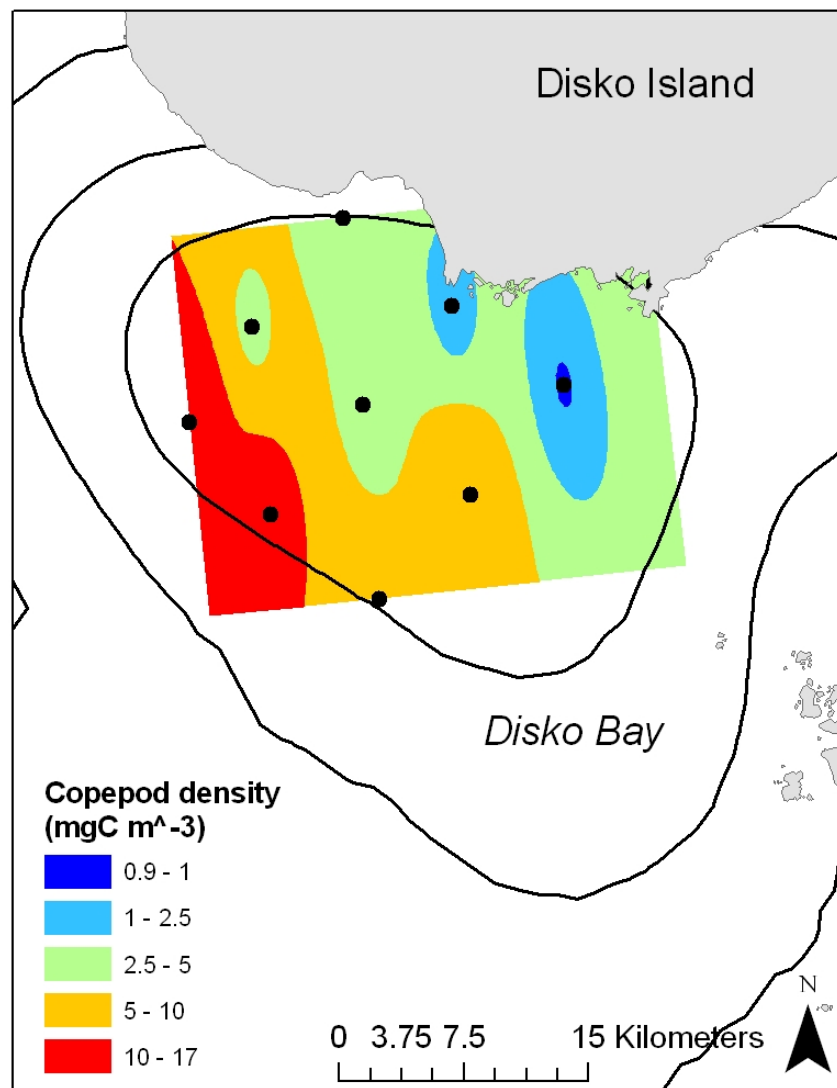


Fig 8 ab. Biomass of copepods between 0 and 200 m in April and May 2005. Zooplankton were sampled in 50 m increments of the water column at 9 standard stations. Not all stations had depths up to 200 m therefore some data are missing. Units are mgC m^{-3} .

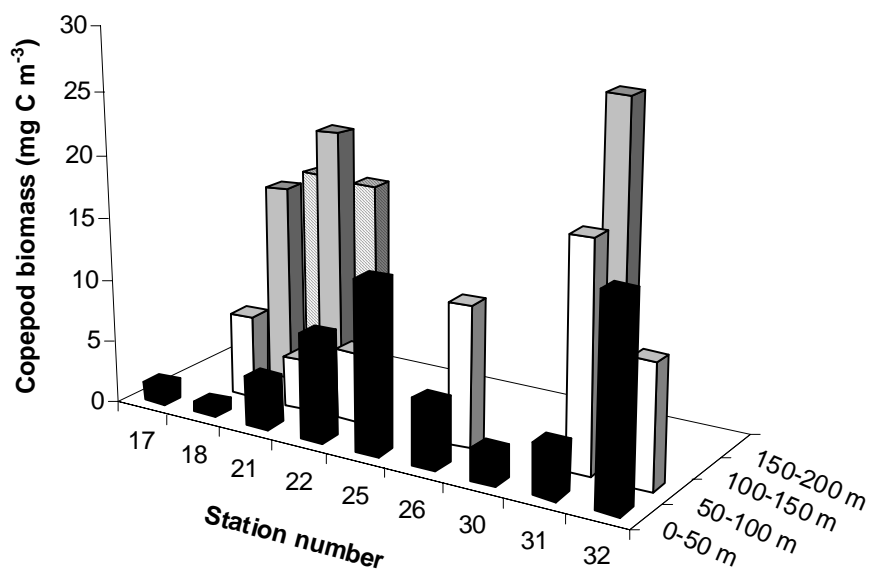
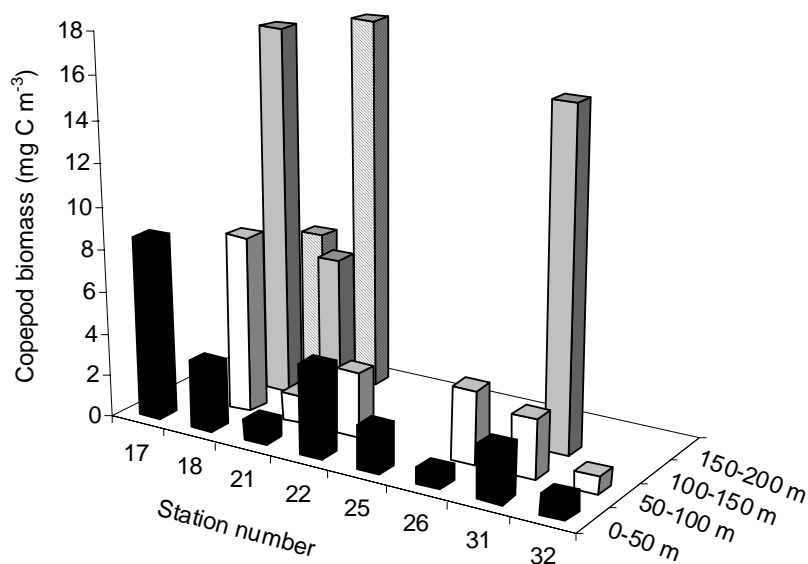


Fig 9. Depth distribution of log zooplankton biomass (mgC m^{-3}) in the Fortune Bay, April 2006. Bottom samples taken < 1 km from the coast in Disko Bay.

