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An estimation of walrus (*Odobenus rosmarus*) predation on bivalves in the Young Sound area (NE Greenland)

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The total consumption of bivalve prey by walruses (*Odobenus rosmarus*) in the important inshore summer feeding area Young Sound (about 74˚ N) in Northeast Greenland was estimated. To determine relative area use, the movement and activity of three adult male walruses with satellite transmitters were studied during the open water season in 1999 and 2001. Because one of the animals was tracked during both years the study covered a total of four "walrus seasons". Overall, the animals used ca. 30% of the time in the water in the inshore study area in Young Sound. The remainder of time was used along the coast north and south of Young Sound and offshore in the Greenland Sea. Information on the total number of walruses using the area (n=60), occupancy in the study area, and estimates obtained from satellite telemetry on the number of daily feeding dives (118-181/24 h at sea), was used to calculate the amount of bivalve food consumed by the walruses during a total of 1620 "walrus feeding days" inshore in Young Sound. Depending on the applied estimator of number of feeding dives, the estimated consumption by walruses of shell-free (SF) bivalve wet weight (WW) during the open water period range between 111 and 171 tons. Based on estimates of mean total body mass (TBM: 1000 kg) of walruses using the area and daily *per capita* gross food intake, the corresponding estimate of consumption by walruses is 97 tons SF WW. Daily feeding rates in walruses (6-7% of TBM) indicate that an estimate of total predation of around 100 tons SF WW per year is plausible.

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Introduction

Major climatic changes in the Arctic due to global warming may affect walruses (*Odobenus rosmarus*) in various ways. Kelly (2001) suggested that a decreased extent of summer sea-ice might negatively impact the ability of Pacific walruses (*O. r. divergens*) to obtain food in the Beaufort and Chukchi Seas. Born et al. (2003) hypothesized that in areas such as eastern Greenland, Svalbard and the Canadian High Arctic archipelago where Atlantic walruses (*O. r. rosmarus*) feed intensively inshore, a reduced ice cover may positively affect the walruses by allowing them access to their feeding areas for a longer period of time. Furthermore, an extension of the duration of the open water period may enhance marine productivity in general (Rysgaard et al. 1999).

In the eastern Atlantic Arctic, including the East Greenland and Svalbard areas, the ice cover has decreased during the last 2-4 decades both in thickness and extent due to global warming (Rothrock et al. 1999, Parkinson 1992, 2000, Comiso 2002). Temperatures have increased in the East Greenland – Svalbard area since the 1960s (Førland et al. 2002, Hanssen-Bauer 2002). Furthermore, a continued dramatic temperature increase and associated reduction in ice cover in the East Greenland area are predicted during this century (Rysgaard et al. 2004).

To evaluate the effects of the reduced ice cover on the Arctic marine ecosystems and their productivity, a multi-disciplinary study CAMP (Changes in the Arctic Marine Production) was initiated in 1995 (e.g. Rysgaard et al. 2000). The focal site of this study is Young Sound (ca. 74˚ 15´ N) in Northeast Greenland where a small group of walruses feed intensively on the inshore mollusk banks during summer. Because walruses are a conspicuous and important component of this ecosystem it was necessary to quantify their trophic role.

The stenophagous walruses are an important component of many High Arctic marine ecosystems where they predate on the benthic invertebrate fauna in coastal waters (e.g. Vibe 1950, Fay 1982, Oliver et al. 1983). Although walruses may feed on a variety of bottom-dwelling invertebrates, only a few bivalve species – usually *Mya sp.*, *Hiatella sp.* and *Serripes sp.* – make up the bulk of their diet (Vibe 1950, Fay 1982, Fay et al.

1984, Sheffield et al. 2001). The Young Sound study area has a rich benthic infauna that includes abundant quantities of these three and other walrus food items (Sejr et al. 2000, 2002, Sejr 2002, Born et al. 2003).

A small group of walruses, genetically distinct from the neighboring Svalbard and West Greenland groups (Andersen et al. 1998, Born et al. 2001) lives all year round in eastern Greenland where they are mainly distributed north of about 72˚ N (Born et al. 1997). Apparently, the walrus sub-population in eastern Greenland was on the verge of extinction in the 1950s due to over-exploitation by European whalers and sealers. However, since its protection in 1956 the East Greenland sub-population of walruses has shown signs of a slow increase (Born et. al. 1995, 1997, Witting & Born in press).

Two main areas are known where East Greenland male walruses concentrate to feed during summer: The Dove Bay area (76 - 77˚ N) and the Young Sound area (Fig. 1). The only two regularly used terrestrial haul-out sites in Greenland are found in these areas: Lille Snenæs in Dove Bay, and the island of Sandøen in Young Sound. Females are distributed along the coast farther north (Born et al. 1997). In recent years up to about 50 adult male walruses have been observed hauling out simultaneously on Sandøen (ibid., Born & Berg 1999).

Based on direct underwater observations of feeding walruses and satellite-telemetered information on diving activity, Born et al. (2003) estimated the amount of food ingested per single feeding dive and during a typical feeding trip.

In the present study we estimate the total predation pressure exerted by walruses on the bivalve population of the Young Sound area during the open water season. This is done by combining information on (1) movement and diving activity in Young Sound of individual walruses equipped with satellite-linked transmitters (this study), with (2) information on food ingested per dive and daily *per capita* feeding rate (Born et al. 2003), and (3) an estimate of number of walruses frequenting the area during the open water period (L.W. Andersen & Born, unpubl. data).

Materials and methods

The study animals

During August 1999 and July 2001 three individual adult male Atlantic walruses that hauled out among other male walruses on the beach of Sandøen (74° 15′ 30′′ N, 20° 18′ 00′′ W) in Young Sound (NE Greenland) were immobilized with etorphine (Born & Knutsen 1990a, Griffiths et al. 1993); Table 1. Estimates of total body mass (TBM) of these animals were obtained from equations on TBM versus standard body length and girth in Knutsen and Born (1994); Table 1. Their approximate age was estimated from a "tusk circumference-at-age" relationship obtained from walruses sampled in NW Greenland (Circumference in cm at basis = 3.0 (SE: 0.94) + 20.5 (SE: 2.57) $*$ (1-exp[-0.068(SE:0.02) $*$ age in years])).

Animal 6481 was tracked in 1999 and 2001 (4344); Table 1. Because its movements and diving activity differed in the two seasons it is treated as two different "cases" in the analyses of activity. Hence, a total of four individual "walrus seasons" were included in the study.

Tracking of movement

During immobilization, a satellite-linked radio transmitter was attached to one of the animal's tusks as described in Born and Knutsen (1992) and Gjertz et al. (2001). Two different types of satellite transmitters were used. In 1999 and 2001, respectively, a ST-10 transmitter was put on an individual that was tracked in both years. In 2001, a SPOT-2 was fitted to the tusks of two other walruses (Table 1). Wildlife Computers (Seattle, USA) manufactured all transmitters.

All the transmitters were able to provide data on location, but their sampling protocols for collection of sensor data were different (*cf.* section "Activity data").

The GIS software ArcView 3.2a was used for mapping the movement of the walruses. For analyses of movement and area use (*cf.* Harris et al. 1990) all position data of all quality classes were run through the PC-SAS®ARGOS-filter that chooses the most plausible location between the ARGOS primary and alternate locations based on minimum distance from the previous chosen location irrespective of the class (V.5.0, D.Douglas USGS, Alaska Science Center, 100 Savikko Road, PO Box

240009, Douglas, AK 99824, USA, unpubl. method). The parameters used during filtering were: Maximum Redundancy was (Distance, rate, angle filter) = 5 km. Minimum movement rate = 10 km/h. Rate coefficient = 15.

Activity data

In the present study, the area for which feeding by walruses was quantified encompassed the areas in Young Sound west of Sandøen and north of 74˚ 14´ N (i.e. on the northern coast of Clavering Ø due south of Sandøen). For each animal the approximate time spent inside (i.e. ”total time spent inshore”) and outside the study area during the open-water season was inferred from the satellite-telemetered locations. Time spent inshore for an animal was defined as fraction of days with locations in Young Sound west of Sandøen of all days monitored during the open water period.

The animals were tracked for different periods of time (Table 1) but their feeding activity was only described and quantified for the open water season (for periods monitored see Table 2).

The ST-10 transmitter used in 1999 was able to collect diving data to a depth of 250 m whereas that deployed in 2001 had a maximum depth range of 500 m (Table 1). Maximum dive depth of the SPOT-2 transmitters was not specified.

For the ST-10 units, information on haul-out time (duration of individual haul-outs and % of time hauled out) was collected via ”timelines”(TIM) that stored data on the status of the salt-water switch (SWS; i.e. dry versus wet) in the course of 24 h in 20 min increments (Born et al. 2002, 2003). Blocks of 24-h timelines were transmitted every 40 transmissions.

The SPOT-2 transmitters were not able to collect dive data or information on the activity of the SWS. For these transmitters, the haul-out time was inferred from temperature data and locations. These units transmitted temperature information summed in 6-h blocks. The temperature histograms were stored in 14 user-defined intervals. For the present purpose, all 6-h blocks in which the temperature was 4 ˚C or higher were assumed to represent a period where the animal was hauled out and exposing the sensor to its own or another walrus’ body-heat or in air temperatures. Mean temperatures in

Young Sound are below freezing 9 months of the year and only the months June to August have a positive mean air temperature of up to 4 ˚C (Rysgaard et al. 2004). In case a 6-h histogram both contained values below and above 4 ˚C, it was assumed that the walrus was hauled out if ≥75% of the time was used at ≥4 ˚C (only < 3% of all 6-h blocks were categorized as representing a haul-out period based on this criterion). The reception during the same periods of good quality locations (location class 3 or 2; *cf.* Harris et al. 1990) was regarded as a confirmation of the fact that the animal was actually hauled out.

Percentage of time spent in water inshore was determined as ”total time spent in the study area minus percentage of time hauled out”.

The ST-10 transmitters sampled time and pressure (depth) every 10 sec. These data were stored in 6-hour blocks and then relayed to the satellite during the following 24 hours. Three types of dive data were used in the present study: (1) number of dives per time unit, (2) Duration of individual dives, (3) daily maximum dive depth (MDD), and (4) time at depths (TAD). Dive data were stored in 14 user-defined intervals that later were organized in the following intervals for analysis: 0-6 m, >6 m. For analyses of diving activity (i.e. number of dives to different depths), haul-out time was extracted from the dive data.

Heavy floes of multi-year ice come into Young Sound from the Greenland Sea during summer. Scouring of the sea floor by this ice and in some cases by icebergs have resulted in relatively low densities of bivalve infauna < ca. 6 m depths along the shores (Sejr et al. 2000; Sejr 2004). It was therefore assumed that dives shallower than 6 m depth represented traveling and social activity whereas all dives deeper than 6 m depth were feeding dives.

The number of feeding dives per 24 h was determined in two ways: (1) the number of dives exceeding 6 m was extracted from the ST-10 satellite transmitters and the number of dives below 6 m/24 h in water was calculated. In this analysis, which only included days spent inshore, all 6-h blocks with no dives (= the animal was hauled out) were omitted; (2) the number of dives of between 5 and 7 min duration (i.e. typical feeding dives; Born et al. 2003 and references therein) were summed for all inshore days

and the average number of 5-7 min long dives per 24 h at sea ("wet h") was calculated omitting 6-h blocks where the animal had not dived (i.e. was hauled out).

Number, age composition and TBM of walruses

The group of walruses using the Young Sound study area during any summer was assumed to number 60 individuals on average. This estimate were based on (1) genetic identification using 11 nuclear markers (i.e. microsatellites) of 38 individuals among 84 biopsies taken from walruses at Sandøen during August 2002, and 81 individuals among 185 biopsies collected there in 2004 (L.W. Andersen and E.W. Born, unpubl. data), and (2) maximum day counts of 47 in 1991 (Born et al. 1997) and 48 in 1994 (Born & Berg 1998).

We estimated the average TBM of the walruses in Young Sound from ID-photos taken at Sandøen in 2002 and 2003. The method used was: The tusks of male walruses grow throughout life (Mansfield 1958) and may therefore serve as a proxy for age, and hence TBM (cf. Knutsen and Born 1994). Individual tusk length was estimated for 27 male walruses that were individually identified from ID-photos taken on Sandøen during August 2002. Furthermore, individual tusk length was estimated from ID-photographs taken of 36 males among a record of 37 walruses that hauled out in one group on Sandøen on 1 and 2 August 2003 (L.Ø. Knutsen and E.W. Born, unpubl. data). On good "en face" and/or "profile" photos the length of an individual´s tusk **(**from lip to tip) was estimated by comparing tusk length with the width of the eye (or the eye slid; 4-5 cm). A "TBM vs. tusk length" (i.e. gum to tip; "clinical crown") relationship was established based on information on TBM and tusk length in 20 individual Atlantic male walruses from Hudson Bay (Loughrey 1959 table I: n = 8), NW Greenland (Born and Knutsen, unpublished; n = 9), and NE Greenland (Born and Aquarone, unpubl.; n=3). Tusk lengths ranged from 0 to 47 cm, and TBM from 93 to 1629 kg. A quadratic hyperbola ($Y = Y_0 + ax + bx^2$) gave the best fit (r^2=0.84) to these TBM vs. tusk length data. TBM (kg) = 193.18 (SE: 95.53) + (16.86 (SE: 9.16)* tusk length (cm)) + (0.188 (SE: 0.20) * tusk length^2). To make our lip-to-tip lengths comparable to gum-tip lengths, 15% was added to our lip-to-tip estimates to account for that part of the tusk that was hidden under the lip

during the photographing (i.e. an estimated 4 to 7 cm upper part of the tusk was covered by the lip). These corrected tusk lengths in walruses at Sandøen and the "TBM vs. tusk length" relationship were then used to calculate individual TBM of walruses photographed on Sandøen in 2002 and 2003.

Estimates of shell-free (SF) bivalve wet weight (WW) biomass and dry matter (DM) obtained during single feeding dives were obtained from Born et al. (2003).

The duration of the open water season (i.e. time from break up of the fast ice in spring until formation of fast ice in the fall), in which walruses have access to the inshore mollusk banks in Young Sound, was 76 d in 1999 and 108 d in 2001 (Rysgaard, in litt. 2003). For simplicity, an open-water period of 90 d is assumed in the calculations.

Data on the total area of suitable walrus feeding habitat in Young Sound between Sandøen and Zackenberg from the coast line to 60 m depth (Fig. 1) were extracted from Rysgaard et al. (2003: table 1).

Information on biomass and production of important bivalve prey in Young Sound was obtained from M. Sejr (*in litt.* 2004).

Estimation of walrus consumption of bivalves in Young Sound

The total amount of bivalves consumed by the walruses in Young Sound during the open water season was estimated by two methods:

(1) Information was combined on (a) relative time in the Young Sound study area during four "walrus seasons" by three walruses that were tracked by use of satellite telemetry, (b) satellite-telemetered information on diving activity, (c) estimates of food ingested during single dives, (d) total number of walruses hauling out on Sandøen in Young Sound, and (e) total duration of the open water period.

(2) Information was combined on (a) the average TBM of walruses using Young Sound, (b) food consumed (6.0% of TBM/walrus/24 wet h, 95% CI: 4.2-7.5; Born et al. 2003), (c) total number of walruses in Young Sound, and (d) total duration of the open water period.

Results

The study area

The Young Sound study area is described in depth in Rysgaard et al. (2003) and Born et al. (2003). For the purpose of this study it is important to notice that a sill across the fjord by Sandøen divides Young Sound into an offshore and inshore area. Inshore, along the coast west of Sandøen up to Zackenberg (Fig. 1) there is an abundance of shallow water banks rich in walrus food items (e.g. Sejr 2002, 2004). Further inshore (i.e. west of Zackenberg) the fjord is > 60 m. Walruses are not seen in this area and as the study animals did not enter this part of the fjord it is likely not good walrus feeding habitat. Hence, for the quantification of bivalve food consumed by walruses in Young Sound only the areas around and west of Sandøen (Fig. 1) up to Zackenberg are considered (i.e. areas 1-3 in Rysgaard et al. 2003 table 1). In this part of the fjord the total area down to 60 m is 50.964 km^2.

The study animals

The estimated TBM and individual age of the three adult male walruses that were tracked by use of satellite telemetry during 1999 and 2001 ranged between ca. 950 and ca. 1400 kg and ca. 24 and ca. 29 years, respectively (Table 1).

Movement and area use

Animal 6481 was tracked from instrumentation on 23 August on Sandøen until 21 November 1999. During this period it used Young Sound but also moved north and south along the coast (Fig. 2). The reception of several high-quality locations (location class = 3) on the southwestern coast of Sabine Ø and from the southeastern coast of Clavering Ø indicated that 6481 also hauled out on land at these places. In 1999 this walrus spent

about 44% of the time inshore in Young Sound either hauling out on Sandøen or in the water (Table 2).

The same individual was tracked in 2001 as 4344 from 24 July until 4 September (Table 1). However, after filtering of the locations its movement could only be reliably described until 2 August (Fig. 3) until which date it remained inshore (Table 2).

Animal 11272 was tracked from 27 July until 14 October 2001 during which time it made excursions offshore in the Greenland Sea as well as north and south of Young Sound (Fig. 4). Judged from the locations, 11272 spent about 22% of the time before formation of fast ice in the study area (Table 2).

Walrus 6482, which was tracked between 28 July and 24 October 2001 also made trips from Sandøen north to the Sabine Ø area and south to the southern coast of Clavering Ø (Fig. 5). This animal used about 57% of the open water period inside the Young Sound study area (Table 2).

Overall, the locations indicated that the four walruses used a weighted average of about 44% of the time in the Young Sound study area (Table 2). When at sea in Young Sound, the locations indicated a clear preference for the areas in northern parts of the fjord where water depths are <40 m (Figs 2-5).

Haul-out and diving activity

During the open water period the four walruses hauled out for between ca. 21 and ca. 66% of the time. Overall, haul-out time averaged 31.4% (Table 3). If individual haul-out time is subtracted, the walruses spent between about 11 and about 45% of the time in the water inside the study area (Table 2). Overall, the satellite telemetered information indicated that on average the walruses spent about one third (29.5%) of the open water season in the water in the Young Sound study area (Table 2).

Data on diving activity during the open water season were only available for animal 6481/4344. For both years and all months combined, an average of ca. 32% of the "at sea" time was spent between 0 and 6 m depth (about 11% of this time was used at the surface; i.e. SWS dry), and the remainder of the time was used at depths below 6 m (Table 4). Less than 1% of the time was used at depths below ca. 40 m.

About 80% of all dives inshore went to depths of 6 m and deeper. During the different months the animal made between 100 and 198 dives/24 wet h below 6 m, with an average of 181 dives/24 wet h (Table 5). Less than 1% of the dives went deeper than ca. 40 m.

The duration of a walrus feeding dive is usually 5-7 min (Born et al. 2003 and references therein). During the inshore period, about 61% of all dives of 6481/4344 lasted between 5 and 7 min (ca. 77% of all dives were between 4 and 8 min in duration), Table 6. When inshore, the animal made an average of about 118 dives of 5-7 min duration per 24 h. Less than 2% of the dives had a duration above 8 min.

On days when 6481/4344 was inshore, the daily maximum depth readings averaged 35.4 m (sd = 24.6, range: 14 – 86 m, n = 7 days with maximum dive depth data) in 1999, and 26.5 m (sd = 7.1, range: 20 – 36 m, n = 8) in 2001, which is in accordance with direct observations (Rysgaard and Ehlmé, pers. comm.) that walruses in Young Sound mainly feed on the shallow water bank along the shores. In none of the years did the maximum dive depths differ between inshore and offshore days (unpaired t-tests; $P > 0.05$). Walrus 6481/4344 made a maximum depth to 136 m on 30 August 1999 at 74˚40´ N and 18˚ 34´ W (i.e. outside Young Sound).

The number of walruses in Young Sound

The number of animals hauling out on Sandøen likely reflects the number using Young Sound and adjacent areas for feeding during summer. Mainly adult males haul out on Sandøen, and observations of females or immature individuals are rare. However, during the summers 2001-2004 the occurrence on Sandøen of females and young on has become more frequent (Born et al. 1997, Born et al. 2000, Born unpubl. data).

Opportunistic and systematic observations (Born & Berg 1999, Born unpubl. data) of the number of walruses hauled out at Sandøen have been carried out since 1983. The daily maximum number of hauled out individuals ranged between 3 and 48. The highest numbers were recorded in 1991 (47) and 1994 (48) (Born et al. 1997, Born & Berg 1999). The maximum number seen on one occasion in late July and August 1998-2003 varied markedly (1998: 28, 1999:9, 2000: 22, 2001: 19, 2002: 19, 2003: 37; Born

& Berg 1999, Born et al. 2000, Acquarone et al. 2001, Born unpubl. data). In 1999 when the lowest number was observed, unusually much pack ice coming from the Greenland Sea occurred in Young Sound. Sometimes this ice blocked the beach at the walrus haul-out probably precluding access to the haul out. However, during all seasons it was clear from observations of individually recognizable animals (*cf.* Born et al. 1997 for methods) that the number of walruses frequenting the haul-out during August was higher than the highest number seen on any single occasion. This was confirmed in 2002 and 2003 when the daily maximum count during the period late July – late August was 19 and 37, respectively, whereas genetic identification *post hoc* revealed that a total of 38 and 81 different animals used the haul-out during the same period (L.W. Andersen and E.W. Born, unpubl. data).

Average TBM of walruses in Young Sound

Based on photos of 27 male walruses that were individually identified in 2002, the estimate of the average TBM of walruses at Sandøen was 1068 kg (sd=295; range: 595-1571 kg). The corresponding estimate for 2003 was 970 kg (sd=341; range: 296-1656 kg). However, for convenience we use an average TBM of 1000 kg for the calculations of food consumption in Young Sound.

Estimation of the walrus consumption of bivalves in Young Sound

For the calculation of bivalve biomass consumption by walruses inshore in Young Sound we assume that a group of 60 walruses have access to the mollusk banks west of Sandøen during an open-water season usually lasting about 90 days. Given the average fraction of the total time spent by the walruses "at sea" inside this study area (ca. 30%), an estimated total of 1620 "walrus feeding days" are spent inshore in Young Sound (Table 7).

Method I

Based on the estimates of the daily mean number of dives to 6 m and deeper and number of dives of between 5 and 7 min duration, the walruses make a total of 191 160 to 293 220 feeding dives, in the Young Sound study area during the open water season.

Using the estimates on number of bivalves, SF dry matter and wet weight, consumed per feeding dive (Table 7), the estimates (two methods of determining number of feeding dives, Table 5 and 6) of the total number of bivalves consumed inshore in Young Sound during the open water season ranged from ca. 10 to ca. 16 $* 10^6$ (Table 7). The estimates of the corresponding amounts of bivalve DM and WW were ca. 29 to ca. 44 tons, and ca. 111 to ca. 171 tons, respectively (Table 7).

Method II

The daily mean gross food consumption was ca. 60 kg/walrus/24 wet h (95% CI: 42-75 kg/walrus/24 h) and the corresponding estimate of the total amount of SF bivalve WW consumed by walruses during the open water season was ca. 97 tons (Table 7).

Daily feeding rates in walruses of 6-7% of TBM (Born et al. 2003, Acquarone 2004) indicate that the estimates of 111 tons (*Method I*) and 97 tons (*Method II*) are the most plausible.

Estimation of the walrus consumption of bivalves in Young Sound

The estimate of the total consumption by walruses during the open water season of ca. 100 tons wet matter (i.e. 111 and 97 tons, respectively; Table 7, I and J) corresponds to the removal of ca. 1.97 g/m^2 SF bivalve WW down to 60 m depth in Young Sound (total area: ca. 51 km^2).

The standing biomass and annual production in Young Sound of the two important walrus food items *Mya sp.* and *Hiatella sp.* are substantial (biomass and production of *Serripes sp.* were not determined). Between 0 and 60 m depth in the areas between Sandøen and Zackenberg the SF WW biomass and annual production of these

two species taken together are ca. 243 g/m^2 and 2.13 g/m^2 * year, respectively (Sejr 2004). Hence, our estimate of walrus predation during the open water season amounts to ca. 0.8 % of the standing biomass of *Mya sp.* and *Hiatella sp.*, and ca. 92 % of the annual production of these bivalves. However, it must be kept in mind that in Young Sound the walruses also forage on other bivalves and benthic invertebrates (Born et al. 1997, 2003).

Discussion

Numbers and TBM

The estimate of average TBM in this study was 1000 kg. The estimate of average TBM differed slightly between 2002 and 2003. However, because the 27 individually identified walruses in 2002 likely were a non-representative part of the group (ID characters such as scars, knobs and cracked tusks are typical in old walruses; cf Born et al. 1997), we believe the estimate of average TBM based on all animals in the group in 2003 to be more representative. The majority of walruses using Sandøen and Young Sound are adult males. Asymptotic TBM in males from NW Greenland was 1114 kg (Knutsen and Born 1994). This indicates that the average TBM used in the present study is reasonable.

Movement

The area of interest to the multi-disciplinary study of marine productivity has been defined as particularly the areas between Sandøen and Basalt Ø (Rysgaard & Glud 2004). This is also the area in which a variety of marine biological studies have been conducted since 1995 (e.g. Rysgaard et al. 1996, 1998, 1999, Sejr et al. 2000, 2002) and for which an overall "carbon/energy" flow-budget will be calculated (Rysgaard & Glud 2004). However, the general scarcity of "at sea" locations received from the walruses tracked in the present study only allowed for the determination of time in Young Sound west of Sandøen to Zackenberg and not a sub-division of the time-budget in this area. The satellite-derived locations during the four "walrus seasons" indicated that walruses on

average spend about 30% of the open water season inshore in Young Sound with a clear preference for the northern shore west to Zackenberg.

During the study period the animals also used other feeding locations south, east and north of Young Sound. The latter area (i.e. Sabine Ø – Lille Pendulum Ø area) is a well-known walrus foraging habitat (Born et al. 1997). In other studies of movement during summer, the walruses also regularly moved ca. 80 km or farther away from the haul-out (Born & Knutsen 1992, Hills 1992, Wiig et al. 1996). Clearly, walruses use several alternative feeding grounds in the vicinity of their traditional haul-out.

Usually the fraction of good quality locations received from walruses that are hauled out is relatively high whereas fewer locations usually of lower precision are received from animals that are at sea (Born & Knutsen 1992, Jay et al. 2001). Walruses spend proportionally much time submerged (e.g. Wiig et al. 1992, Born & Knutsen 1997, Born et al. 2003) and do not always get the salt-water switch of the transmitter out of the water when ventilating (Born, unpubl. data), resulting in no or to few signals being transmitted. This may imply that relatively few locations are transmitted from areas where walruses are at sea and actively foraging. This fact obviously will influence the ability to proportionate time in different areas based on locations. On the other hand, when subtracting cases when the animals were hauling out, we believe that a general picture of relative time spent in various areas "at sea" could be deduced from the locations.

Haul-out and diving activity

We tracked relatively few animals during two open water seasons. However, the activity of the animals that were monitored via satellite telemetry was typical of walruses in general. The animals hauled out for an average of about 31% of the time, which is in close agreement with haul-out times obtained during August-September in other studies of walrus activity involving satellite telemetry (Hills 1992, Born & Knutsen 1992).

We defined dives >6 m as feeding dives. The proportions of the number of dives to these depths were within the range observed in walruses that were studied in August in Dove Bay in 2001. Six adult male walruses equipped with MK-7 dive-recorders (Wildlife

Computers) hauled out for an average of 34% of the time and made an average of 165 dives >6 m/24 "wet" h (range: 108-208 dives/24 h) (Acquarone 2004).

In Young Sound bivalve food items are mainly distributed between 10 and 40 m depth and are less abundant at depths less than ca. 6 due to ice scouring (Sejr 2002, 2004). Visual observations of walruses feeding along the northern coast of Young Sound indicate that they feed between ca. 8 and ca. 34 m (Born et al. 2003). The vast majority of time at depth and dives were between 6 and 42 m which is typical of walruses that are though to be feeding (Gjertz et al. 2001, Jay et al. 2001). Hence, our assumption that activity between 0 and 6 m was mainly associated with traveling, breathing and resting at the surface, and social interactions with other walruses seems sound.

We also quantified the foraging from the number of dives of 5-7 min duration, which is the duration of typical feeding dives in walruses (Wiig et al. 1992, Gjertz et al. 2001, Jay et al. 2001).

In the present study the walruses made an average of 118-181 presumed feeding dives/24 h in the water. Adding "at surface" intervals of ca. 1 min between feeding dives (Born & Knutsen 1997, Born et al. 2003) indicate that the walruses were engaged in diving for food for between 58% (dive duration) and 88% (dives at depth) of their "in water" time. Six adult male walruses that were tracked by use of satellite transmitters in Dove Bay in 1989 were diving for an average of 72% of their "at sea" time (range: 65%-77%; Born & Knutsen 1990b). Similarly, six males studied with MK-7 dive-recorder in the same area were submerged for an average of 66% of the time (range: 34%-84%; Acquarone 2004). This indicates that (1) the activity seen in the present study is typical of walruses when feeding inshore, and (2) that the estimate of total food consumption based on number of 5-7 min dives/24 wet h is plausible, and likely more so than the estimate based on number of dives deeper than 6 m/24 wet h.

It can be assumed that not all dives deeper than 6 m and 5-7 min long resulted in successful feeding. In that case, the amount of food consumed by the walruses is here overestimated to an unknown extent.

Estimates of number of walruses, TBM and food consumption

In the calculations of the number of "walrus feeding days" we assumed that the total group using the area is about 60. This was based on the genetic identification of individuals in 2002 and 2003. Clearly, the number using the area can vary widely between years. The fact that 2003 was a year with unusually little ice in the area probably caused the walruses to use Sandøen as a haul-out intensively. Consequently, many walruses used the haul-out during that season, and we cannot exclude that this inflated our estimate of the average number of walruses using the Young Sound area.

Based on the tracking of admittedly few animals we estimated that at any given time about 20 walruses are foraging in the Young Sound between Sandøen and Zackenberg at depths between 0 and 60 m (total area: ca. 51 km^2). In August 2001, Levermann et al. (2004) studied walrus foraging activity through direct observations within a 1.5 km^2 area at the coast ca. 5 km north of the island of Sandøen. They found that he probability of a walrus being present within the observation area at any given time was 0.47. Hence, provided that the walrus activity in Leverman et al.´s (2004) observation area is representative of the activity in the entire Young Sound walrus foraging habitat considered by us, a simple extrapolation from the observational data indicates that about 16 walruses are foraging in Young Sound at any given time during August ([51/1.5] * 0.47).

We estimated that the average TBM of the walruses in Young Sound is about 1000 kg. This is somewhat higher than average TBM of 512 kg used by Welch et al. (1992) for calculation of walrus feeding in Lancaster Sound (Canada), and 712 kg used by Fay (1982) in Alaska. However, the walruses that feed in Young Sound are nearly all adult males in contrast to the other two areas where all age classes and both sexes are represented at the summer feeding grounds.

For calculation of food consumption (*Method II*) we assumed that the daily gross food intake of walruses in the water is 6% (Born et al. 2003). Fay (1982:table 25) assumed that the daily food consumption of a 1000 kg walrus is 5.7%. Direct measurement of walrus energy expenditure in NE Greenland in 2001, indicated that daily gross food consumption in adult male walruses is 6-7% of TBM (Acquarone 2004). We therefore believe that the estimate of 6% used in this study is realistic.

From direct observations, Levermann et al. (2004) estimated that a total of ca. 2.5 tons of bivalve wet matter was removed in the 1.5 km^2 observation area during the 90 d open water period (ca. 1.7 tons ww/km^2). If applying this estimate to the total foraging area used in the present study, walruses may consume an estimated ca. 87 tons of clam meat in Young Sound during the open water season. This is somewhat less than the consumption estimated by us (100 tons) and indicates that the methods in the present study tended to overestimate the predation by walruses. On the other hand, Levermann et al.´s (2004) study area constituted only ca. 3% of the study area and covered a smaller part of the inshore period.

The impact of the walruses on the bivalve community

A high standing stock of bivalves is present in the study area (Sejr 2004, Sejr et al. 2000, Sejr et al. 2002), which is representative of other inshore ice-covered Arctic areas (Berthelsen 1937, Vibe 1950, Ockelmann 1958, Thomson et al. 1986, Grebmeier et al. 1989, Welch et al. 1992). The estimates of walrus consumption in Young Sound were ca. 0.8% of the standing biomass of the two important food items *Mya sp.* and *Hiatella sp.*, and 92% of their production.

However, the standing stocks and productivity in Young Sound of other walrus food items, for example *S. groenlandicus*, have not been determined. If these are also considered, the inshore bivalve banks in Young Sound represent a richer food source than accounted for in our calculation of predation which is based only on two prey species.

The estimates of gross food intake per dive or per TBM used in the present study were adopted from Born et al. (2003). The estimates were based on three bivalve species that constitute the far most important portion of the walrus diet. However, walrus feed on a variety of benthic food (e.g. Fay 1982) and as pointed out by Born et al. (2003) it cannot be precluded that walruses in Young Sound also feed on other bivalves (e.g. *Astarte sp.*) and invertebrate benthos (e.g. polychaetes, sea cucumbers and gastropods) other than the three species considered. On the other hand, historical observations of the diet of walruses feeding in the vicinity of Young Sound indicate that *M. truncata* and *Hiatella sp.* were principal food items (Peters 1874, Payer 1877a,b) and are also the most

abundant species in the area. Hence the estimates of the present study of walrus ingestion rates inferred from the bivalves studied are likely to be representative.

We conclude that (1) walruses that haul-out on Sandøen only use Young Sound as one of several alternative feeding grounds during summer, and (2) that activity data and information on number of walruses and food ingestion rates indicates that walrus predation in Young Sound is below carrying capacity of the Young Sound study area. This latter conclusion is supported by the fact that historically walruses were more abundant in the area (Born et al. 1997, Witting & Born in press).

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Figure captions

Fig. 1 Map of the study area in northeastern Greenland.

Fig. 2 Movement of an adult male walrus (6481) in Young Sound and adjacent areas in NE Greenland between 23 August and 21 November 1999. Black signatures = locations received during the open water period until 3 October when a dense layer of fast ice had formed west of Sandøen. Gray signatures = locations received after formation of fast ice.

Fig. 3 Movement of an adult male walrus (4344) in the Young Sound area (NE Greenland) between 24 July and 2 August 2001. This animal was tracked as ID no. 6481 in 1999 (Table 1, Fig. 4). Locations were received until 3 September but only locations until 2 August remained after filtering (see Materials and methods).

Fig. 4 Movement of an adult male walrus (11272) in Young Sound and adjacent areas in NE Greenland between 27 July and 14 October 2001. Black signatures = locations received during the open water period until 3 October when a dense layer of fast ice had formed west of Sandøen. Gray signatures = locations received after formation of fast ice.

Fig. 5 Movement of an adult male walrus (6482) in Young Sound and adjacent areas in NE Greenland between 28 July and 24 October 2001. Black signatures = locations received during the open water period until 3 October when a dense layer of fast ice had formed west of Sandøen. Gray signatures = locations received after formation of fast ice.

Table captions

Table 1 Identification code, type of satellite transmitter, date of instrumentation and last re-location, estimate of total body mass (TBM) and approximate age of three different adult male walruses that were tracked in the Young Sound area (NE Greenland) in 1999 and 2001.

Table 2 Estimates of time used at the inshore feeding banks in Young Sound (NE Greenland) by four adult male walruses that were tracked by use of satellite telemetry in 1999 and 2001.

Table 3 Estimates of haul-out time (%) for four adult male walruses when being inshore in the Young Sound area (NE Greenland) in 1999 and 2001.

Table 4 Time (%) spent in different depth intervals (TAD, Time-At-Depth) by an adult male walrus (same individual in both seasons) inshore in the Young Sound area (NE Greenland) in 1999 and 2001.

Table 5 Number of dives and percentage of dives made to different depth intervals by an adult male walrus (same individual in both seasons) inshore in the Young Sound area (NE Greenland) in 1999 and 2001.

Table 6 Number of dives and percentage of dives made in different intervals of dive duration by an adult male walrus (same individual in both seasons) inshore in the Young Sound area (NE Greenland) in 1999 and 2001.

Table 7 Estimates of bivalves, dry matter (DM) and shell-free (SF), wet weight (WW) consumed per dive, total number of walruses using Young Sound, and estimates of total amount of bivalves, DM and WW eaten in the study area by walruses during the open water season. During the open water period a total of 60 walruses used about 30% of their inshore for a total of 1620 ”walrus feeding days”.

Fig. 1

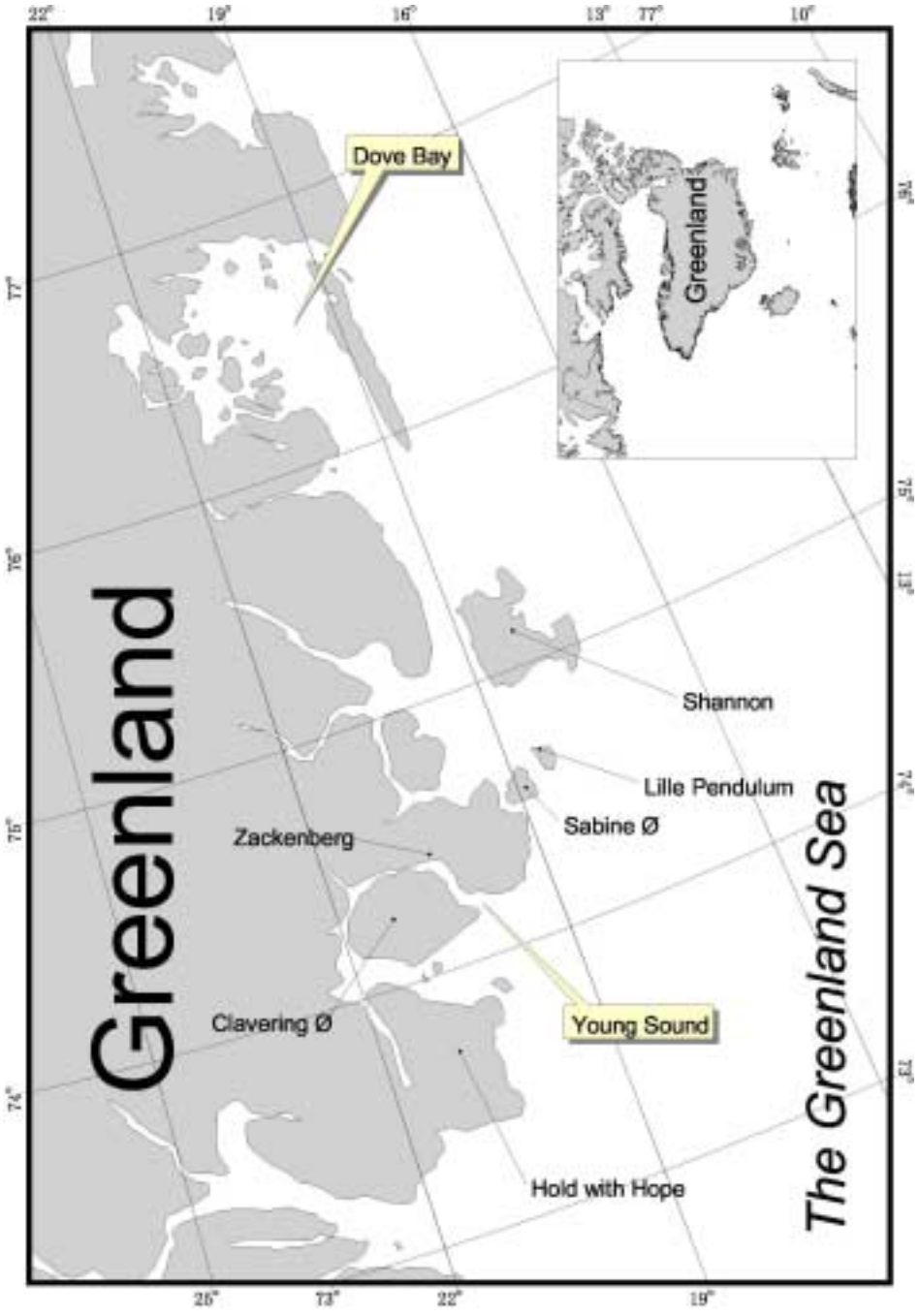
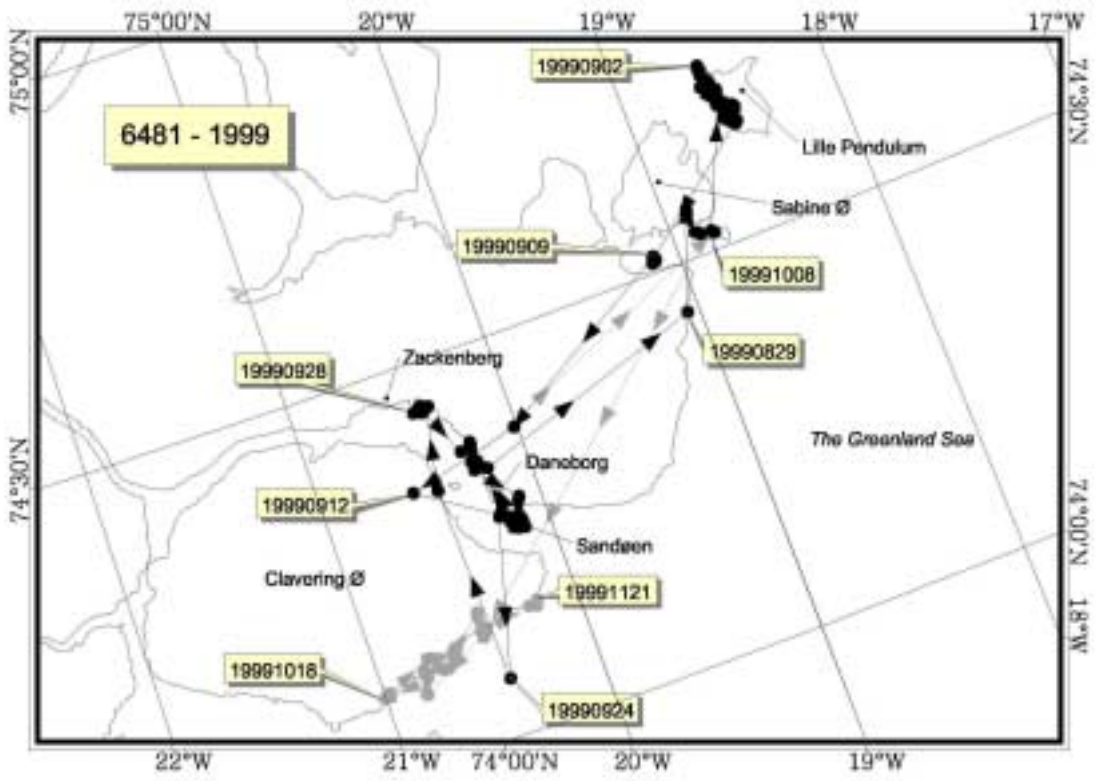

Dove Bay
Greenland
Shannon
Lille Pendulum
Sabine Ø
Zackenberg
Clavering Ø
Young Sound
Hold with Hope
Greenland
The Greenland Sea

Fig. 2


75°00'N
20°W
19°W
18°W
17°W
74°30'N
74°00'N
18°W
22°W
21°W
74°00'N
20°W
19°W
6481 - 1999
19990902
Lille Pendulum
Sabine Ø
19990909
19991008
19990829
19990928
Zackenberg
The Greenland Sea
Daneborg
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Sandøen
Clavering Ø
19991121
19991018
19990924

Fig. 3

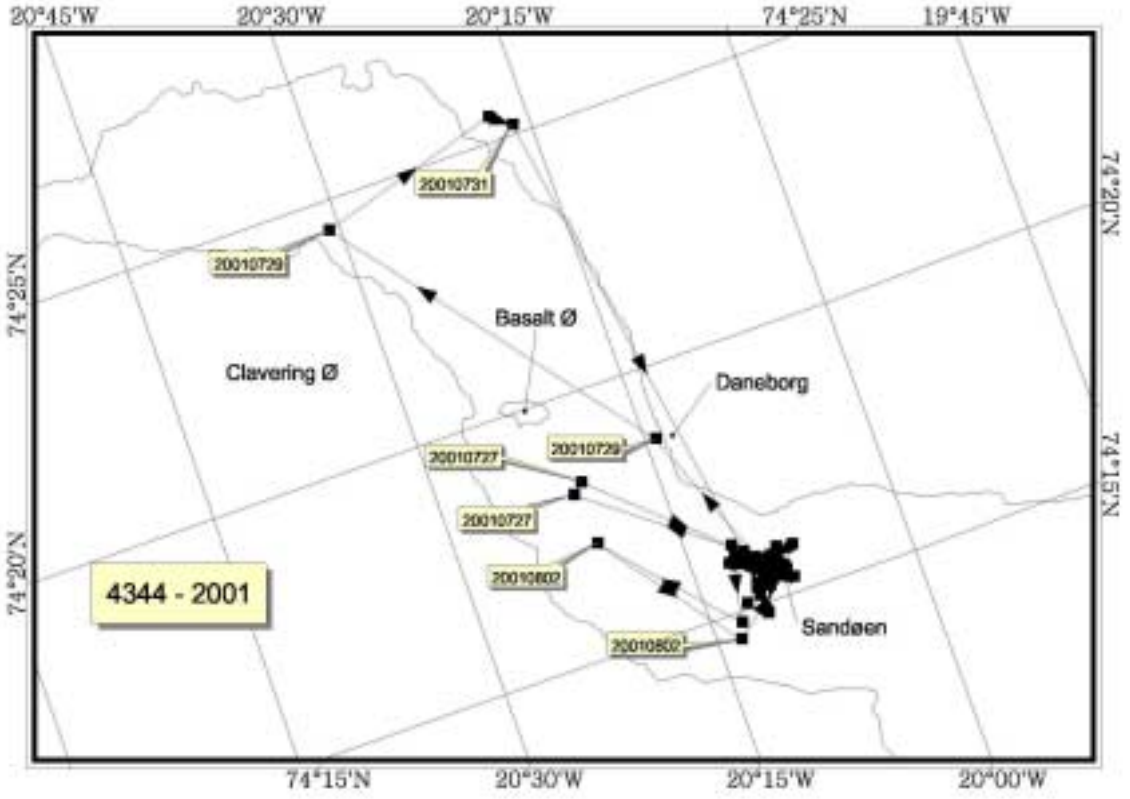
20°45'W
20°30'W
20°15'W
74°25'N
19°45'W
74°25'N
74°20'N
74°15'N
74°15'N
20°30'W
20°15'W
20°00'W
20010731
20010729
Basalt Ø
Clavering Ø
Daneborg
20010727
20010729
20010727
20010802
20010802
Sandøen
4344 - 2001

Fig. 4

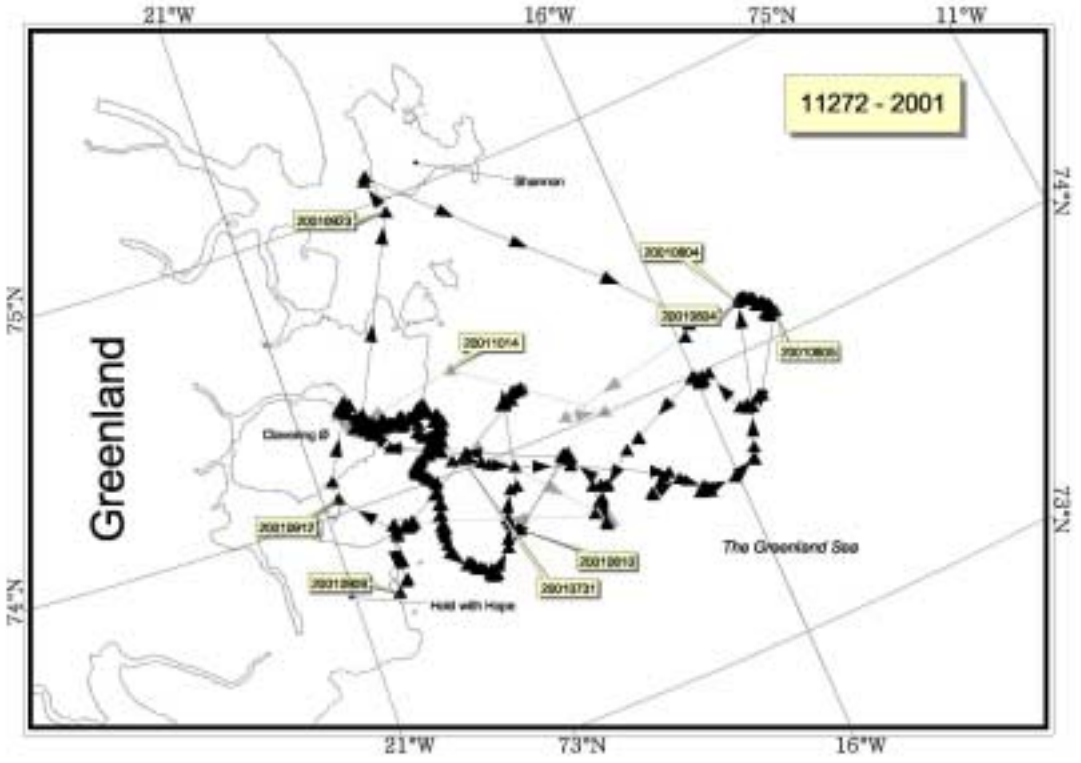
21°W
16°W
75°N
11°W
11272 - 2001
Greenland
Shannon
20010803
20010804
20010914
20010809
Clavering Ø
20010912
20010913
20013731
Hold with Hope
The Greenland Sea
74°N
73°N
21°W
73°N
16°W

Fig. 5

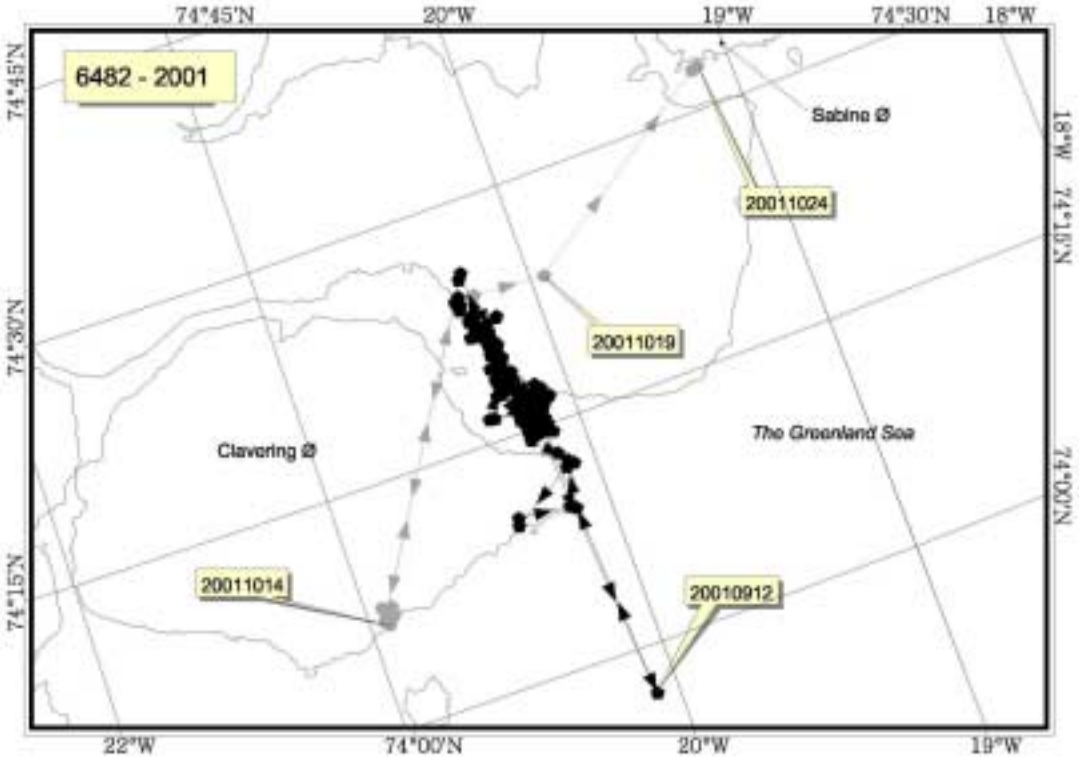
74°45'N
20°W
19°W
74°30'N
18°W
6482 - 2001
Sabine Ø
20011024
20011019
The Greenland Sea
Clavering Ø
20011014
20010912
74°45'N
74°30'N
74°15'N
18°W
74°15'N
74°00'N
22°W
74°00'N
20°W
19°W

Table 1

ID	Transmitter type	Output (Watt)	Depth range (m)	Date of instrumentation	Last location Day-month-year	TBM[2)] (kg)	Age[3)] (year)
6481	ST-10	0.25	250	23 Aug. 1999	21 Nov. 1999	950	24 (at least 13)
4344[1)]	ST-10	0.25	500	24 Jul. 2001	4 Sep. 2001	1200	26 (at least 15)
11272	SPOT-2	0.50	-	27 Jul. 2001	14 Oct. 2001	1400	26 (at least 14)
6482	SPOT-2	0.50	-	28 Jul. 2001	24 Oct. 2001	1100	29[4)]

1: Same animal that was tracked as 6481 in 1999

2: TBM = Total body mass estimated from body dimensions (Knutsen & Born 1994)

3: Age estimated from a "tusk circumference on age" relationship (*cf.* Materials and methods)

4: In 2002, this animal was killed by hunters at the entrance to Scoresby Sound and therefore molar teeth for estimation of age became available. Age was estimated from counting of growth layers groups in tooth cementum following the method of Mansfield (1958).

Table 2

ID	Period monitored	Total[1)] hours monitored	Hours[2)] inshore	% time spent inshore	% of total time spent in the water inshore[3)]
6481	24 Aug.[4)] - 2 Oct. 1999	960	419	43.7	33.0
4344	24 Jul. - 2 Aug. 2001[5)]	228	228	100.0	34.4
11271	27 Jul. - 2 Oct. 2001	1620	357	22.0	10.9
6482	28 Jul. - 5 Oct. 2001	1668	948	56.8	44.9
All	All months, both years	4476	1952	43.6	29.5

1: Period until formation of an ice cover in Young Sound
2: At Sandøen and west of this island
3: Haul-out time subtracted (*cf.* Table 3)
4: Day of instrumentation not included
5: Location received until 4 Sep. but after filtering last validated location was from 2 August 2001

Table 3

ID	Period monitored	% of time hauled out	Total days monitored	No. of 6-h blocks monitored
6481	25 Aug. - 29 Sep. 1999	24.3	16	-
4344	24 Jul. - 2 Aug. 2001	65.6	10	-
11271	1 Aug. - 23 Aug. 2001	50.5	26	97
6482	28 Jul. - 5 Oct. 2001	21.0	70	276
All	All months, both years	31.4	122	-

Table 4

ID	Month	Year	% time at different depths			Days monitored	No. of 6-h blocks
			At surface[1)]	0-6 m[2)]	>6 m		
6481	Aug.	1999	9.2	39.8	60.2	9	30
	Sep.	1999	11.8	29.8	70.2	29	88
	Oct.	1999	7.6	25.1	74.9	4	9
4344	Jul	2001	11.1	31.9	68.1	6	22
	Aug.	2001	15.8	37.2	62.8	2	2
	All	99+01	11.0	31.9	68.1	50	151

1: Time when the salt-water switch was dry

2: Includes time at surface.

Table 5

ID	Month	Year	% of all dives		No. dives	No. 6-h blocks with dive data [1)]	No. of dives beyond 6 m per 24 h[1)]	Dates
			0-6 m	>6 m				
6481	Aug.	1999	20.1	79.9	1798	29	198	23-31
	Sep.		17.7	82.3	4796	86	184	1-30
4344	Jul.	2001	24.6	75.4	1183	22	162	24-31
	Aug.		40.9	59.1	127	3	100	1-2
	All	99+01	19.7	80.3	7904	140	181	-

1: periods of haul-out were excluded

Table 6

ID	Period	Year	% of dives		Total no. of dives[1)]	No. of 6-h blocks monitored	No. of 5-7 min long dives per 24 wet h	No. of days monitored
			5-7 min	4-8 min				
6481	27 Aug. - 2.Oct.	1999	58.3	76.1	1335	27	142	10
4344	25 Jul. - 2 Aug.	2001	66.0	78.2	565	12	124	4
	All	99+01	60.6	76.7	1900	39	118	14

1: Periods with haul-out excluded

Table 7

	Parameter	Mean/estimated value	95% CI	Comments
A	No. Bivalves ingested/dive	53.2	43.0-64.4	Estimated from 10 feeding dives in Young Sound (Born et al. 2003)
B	DM/dive (g)	149.0	112.0-186.0	(Born et al. 2003)
C	WM/dive (g)	583.0	444.0-722.0	(Born et al. 2003)
D	Total no. walrus	60	-	Genetically identified (*cf*. Materials and methods)
E	No. walrus feeding days	1620	-	(duration of open water season, 90 d, * % occupancy * 60 walrus)
F	No. dives/day	118-181	-	Based on Table 5 and 6
G	Total no. of bivalves eaten	$10.2 * 10^6$-$15.6 * 10^6$	-	(A * E * F)
H	Total DM eaten ($*10^3$ kg)	28.5-43.7	-	(B * E * F)
I	Total WW eaten ($*10^3$ kg)	111-171	-	(C * E * F)
J	Total WW eaten ($*10^3$ kg)	97	68-122	Based on mean TBM and a daily food consumption of 6% (95%CI: 4.2-7.5%) of TBM when in water (Born et al. 2003).

DM = Dry Matter; WW = Wet Weight, or wet matter