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

Erik W. Born[1] and Mario Acquarone[2*]

[1]Greenland Institute of Natural Resources, Kivioq 2, Box 570, DK-3900 Nuuk, Greenland
[2]National Environmental Research Institute, P.O. Box 358, DK-4000 Roskilde, Denmark
*Present address: Frue Kirkestræde 5, DK-5000 Odense, Denmark.

Cite as: Born, E.W. & Acquarone, M. 2007. An estimation of walrus (*Odobenus rosmarus*) predation on bivalves in the Young Sound area (NE Greenland). In: Rysgaard, S. & Glud, R. N. (Eds.), Carbon cycling in Arctic marine ecosystems: Case study Young Sound. Meddr. Grønland, Bioscience 58: 176-191.

Abstract

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 carrying 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 spent c. 30% of their time in the water inshore in Young Sound between Sandøen and Zackenberg. The remaining time was spent along the coast north and south of Young Sound and offshore in the Greenland Sea. The total amount of bivalve food consumed in Young Sound by the walruses during a total of 1620 "walrus feeding days" was calculated from 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). 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 ranged 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 (6% of TBM), the corresponding estimate of consumption by walruses is c. 97 tons SF WW. It is suggested that the two lowest estimates of total consumption are the most plausible.

10.1 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 time period. Furthermore, prolonging of the open-water period may enhance marine productivity in general (Rysgaard et al., 1999).

Temperatures have increased in the East Greenland–Svalbard area since the 1960s (Førland et al., 2002; Hanssen-Bauer, 2002). Consequently, the ice cover in the eastern Atlantic Arctic, including the East Greenland and Svalbard areas has decreased

during the last decades in both thickness and extent (Rothrock et al., 1999; Parkinson, 1992; 2000; Comiso, 2002; Comiso & Parkinson, 2004). Furthermore, the dramatic temperature increase and associated reduction in ice cover in the East Greenland area are predicted to continue during this century (Rysgaard et al., 2003).

To evaluate the effects of 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 (see Preface). The focal site of this study is Young Sound (c. 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 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 including abundant quantities of potential walrus food items (Sejr, 2002; Sejr et al., 2000, 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 distributed mainly north of about 72˚ N (Born et al., 1997). Apparently, the walrus sub-population in eastern Greenland was on the verge of extinction around the middle of the 20th century due to over-exploitation by European whalers and sealers. However, since its protection in 1956 this sub-population of walruses has shown signs of a slow increase (Born et al., 1995, 1997; Witting & Born, 2005).

Two main areas are known where East Greenland walruses concentrate to feed inshore during summer: The Dove Bay area (76˚–77˚ N) and the Young Sound area (Fig. 10.1). Two regularly used terrestrial haul-out sites are found in these areas: Lille Snenæs in Dove Bay, and the island of Sandøen in Young Sound. These haul-outs are used mainly by male walruses, while females are distributed along the coast farther north (Born et al., 1997). In recent years, up to 60 (2004) walruses have been observed hauled out simultaneously on Sandøen (ibid., Born & Berg, 1999; M. Acquarone, unpubl. data).

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 excursion from Sandøen.

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 & E.W. Born, unpubl. data). The purpose is to quantify the trophic role of walruses in the Young Sound ecosystem.

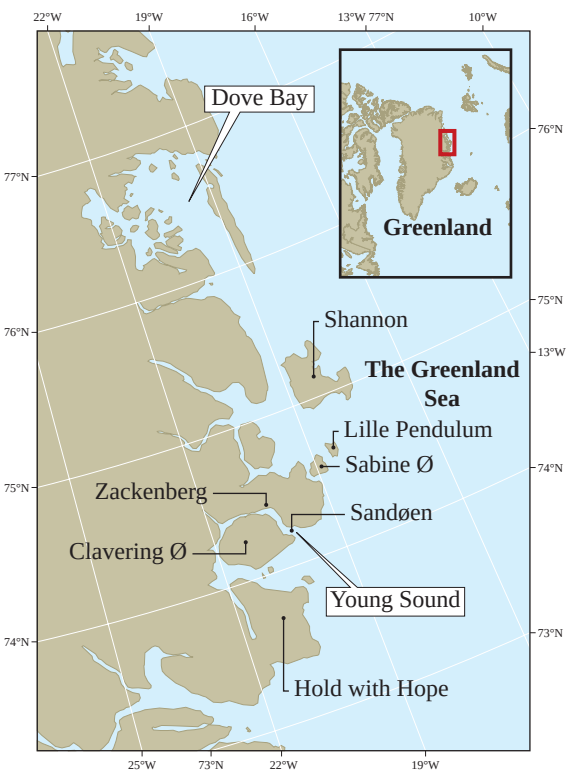

Figure 10.1 Map of the study area in Northeast Greenland.

Table 10.1 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 tracked in the Young Sound area (NE Greenland) in 1999 and 2001.

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)] Tracked as no. 6481 in 1999
[2)] TBM = Total body mass estimated from body dimensions (Knutsen & Born, 1994)
[3)] Age estimated from a "tusk-circumference-at-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 layer groups in tooth cementum following the method of Mansfield (1958).

10.2 Materials and methods

10.2.1 The study animals

During August 1999 and July 2001 three individual adult male Atlantic walruses hauled out among other male walruses on the beach of Sandøen ("The Sand Island"; 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 10.1). Estimates of total body mass (TBM) of these animals were obtained from equations on TBM versus standard body length and girth in Knutsen & Born (1994) (Table 10.1). Their approximate age was estimated from a "tusk-circumference-at-age" relationship obtained from 51 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])).

10.2.2 Tracking of movement

After immobilization of the animal, a satellite-linked radio transmitter was attached to one of its tusks as described in Born & 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 attached to an individual that was tracked in both years. In 2001, SPOT-2 transmitters were fitted to the tusks of two other walruses (Table 10.1). All transmitters (Wildlife Computers, Redmond, Washington, USA) were able to provide data on location, but their sampling protocols for collection of sensor data were different (cf. section 10.2.3).

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 was run through the PC-SAS®ARGOS-filter, which 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).

Animal 6481 was tracked in 1999 and 2001 (4344; Table 10.1). 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.

10.2.3 Activity data

Feeding by walruses was quantified in Young Sound for the areas between Sandøen and Zackenberg, 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 at 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 10.1) but their feeding activity was only described and quantified for the open-water season (for periods monitored see Table 10.2).

Table 10.2 Estimates of time spent at the inshore feeding banks in Young Sound (NE Greenland) by three adult male walruses tracked by use of satellite telemetry in 1999 and 2001.

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 ice cover in Young Sound
[2] At Sandøen and west of this island
[3] Haul-out time subtracted (cf. Table 10.3)
[4] Day of instrumentation not included
[5] Location received until 4 Sep. but after filtering last validated location was from 2 August 2001

The ST-10 transmitter used in 1999 was able to collect diving data to a depth of 250 m, whereas the one deployed in 2001 had a maximum depth range of 500 m (Table 10.1). 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 (Born et al., 2002, 2003). 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 hauled out and exposed the sensor to its own or another walrus' body-heat or ambient 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., 2003; Chapter 3). When a 6-h histogram contained values both below and above 4˚C, the walrus was assumed to be hauled out if ≥75% of the time was spent 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 seconds. This data was 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 unit time, (2) duration of individual dives, (3) daily maximum dive depth (MDD), and (4) time at depth (TAD). Dive data was stored in 14 user-defined intervals, which were later 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 occasionally enter Young Sound from the Greenland Sea during summer. Scouring of the sea floor by this ice and in some cases by icebergs has resulted in relatively low densities of bivalve infauna at depths shallower than c. 6 m along the shores (Sejr et al., 2000; Chapter 7). Dives shallower than 6 m depth were therefore assumed to represent traveling and social activity, whereas all dives deeper than 6 m depth were categorized as 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 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 dives per 24 h at sea ("wet h") was calculated omitting 6-h blocks where the animal was hauled out.

10.2.4 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 was based on (1) genetic identification using 11 nuclear markers (i.e. micro-satellites) 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 & E. W. Born, unpublished data), and (2) maximum day counts of 47 in 1991 (Born et al., 1997), 48 in 1994 (Born & Berg, 1999) and 60 in 2004 (M. Acquarone, unpublished data).

We estimated the average TBM of the walruses in Young Sound from ID photos taken at Sandøen in 2002 and 2003. The following method was used: The tusks of male walruses grow throughout life (Mansfield, 1958) and may therefore serve as a proxy for age, and hence TBM (cf. Knutsen & Born, 1994). Individual tusk length was estimated for 27 male walruses individually identified from ID photos taken on Sandøen during August 2002. Furthermore, individual tusk length was estimated from ID photos taken of 36 males among a record of 37 walruses hauled out in one group on Sandøen on 1 and 2 August 2003 (L. Ø. Knutsen & E.W. Born, unpublished 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 (4–5 cm). A TBM vs. tusk length (measured from gum to tip, i.e. "clinical crown") relationship was established based on information on TBM and tusk length in 20 individual Atlantic male walruses from Hudson Bay (Loughrey 1959, n = 8), NW Greenland (E. W. Born & L. Ø. Knutsen, unpublished data; n = 9), and NE Greenland (E. W. Born & M. Acquarone, 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 with gum-to-tip lengths, 15% was added to our lip-to-tip estimates to account for the part of the tusk concealed by the lip during photography (i.e. an estimated 4 to 7 cm of the upper 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).

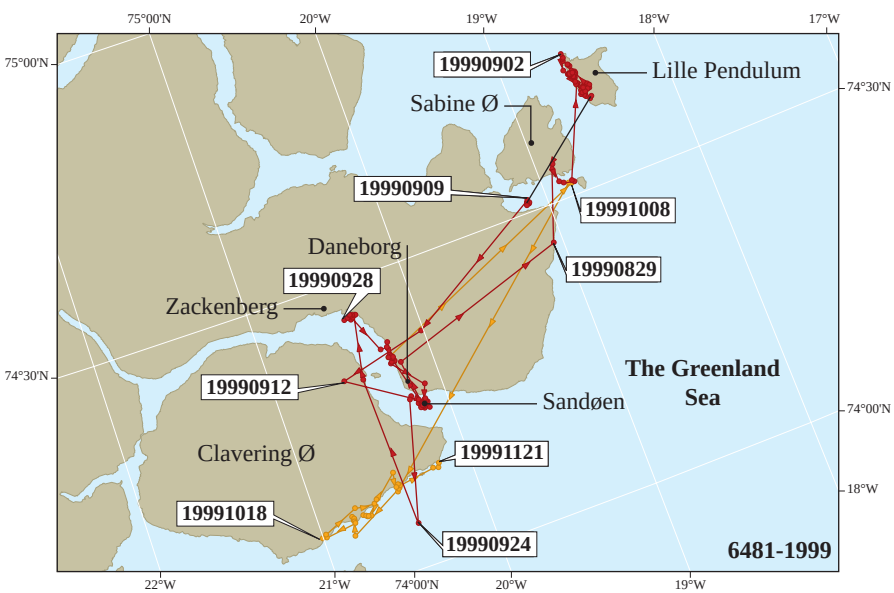

Figure 10.2 Movement of an adult male walrus (no. 6481) in Young Sound and adjacent areas in NE Greenland between 23 August and 21 November 1999. Red tracks = locations received during the open-water period until 3 October when a dense layer of fast ice had formed west of Sandøen. Orange tracks = locations received after formation of fast ice.

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 (Chapter 4). For simplicity, an open-water period of 90 d was used in the calculations.

Data on the total area of suitable walrus feeding habitat in Young Sound between Sandøen and Zackenberg (Fig. 10.2) from the coast to 60 m depth was extracted from Rysgaard et al. (2003, Regions 1, 2 and 3). This area amounted to 50.96 km^2 of which 24.13 km^2 were found between Sandøen and Basalt Ø situated halfway to Zackenberg.

Information on biomass and production of important bivalve prey in Young Sound was obtained from Chapter 7.

10.2.5 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 spent in the Young Sound study area during four "walrus seasons" by three walruses 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 hauled 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. 2002), (c) total number of walruses in Young Sound, and (d) total duration of the open-water period.

10.3 Results

10.3.1 The study area

The Young Sound study area has previously been described 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 at Sandøen divides Young Sound into an offshore and an inshore area. Inshore, along the coast west of Sandøen up to Zackenberg (Fig. 10.2) there is an abundance of shallow-water banks rich in walrus food items (e.g. Sejr, 2002; Chapter 7). Further inshore (i.e. west of Zackenberg) the fjord is much deeper with steep slopes. Walruses are not seen in this area and as the study animals did not enter this part of the fjord it is probably not a favorable 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. 10.2) up to Zackenberg are considered.

10.3.2 The study animals

The estimated TBM and individual age of the three adult male walruses tracked by use of satellite telemetry during 1999 and 2001 ranged between c. 950 and c. 1400 kg and c. 24 and c. 29 years, respectively (Table 10.1).

10.3.3 Movement and area use

Animal no. 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. 10.2). 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 no. 6481 also hauled out on land in these places. In 1999, this walrus spent about 44% of the time inshore in Young Sound either hauled out on Sandøen or in the water (Table 10.2).

The same individual was tracked in 2001 as no. 4344 from 24 July until 4 September (Table 10.1). However, after filtering of the locations its movements could only be reliably described until 2 August (Fig. 10.3), until which date it remained inshore (Table 10.2).

Animal no. 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. 10.4). Judging from the locations, no. 11272 spent about 22% of the time before formation of fast ice in the study area (Table 10.2).

Walrus no. 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 south coast of Clavering Ø (Fig. 10.5). This animal about 57% of the open-water period inside the Young Sound study area (Table 10.2).

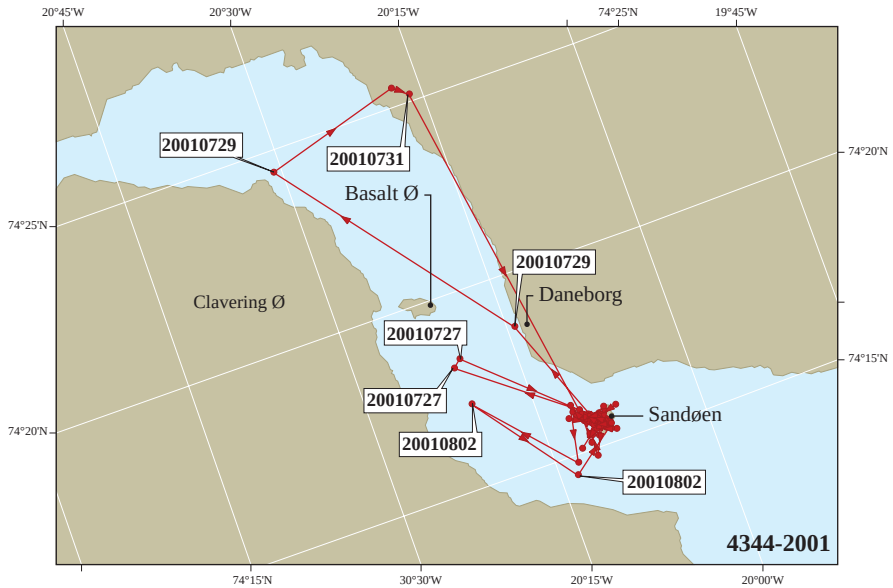

Figure 10.3 Movement of an adult male walrus (no. 4344) in the Young Sound area (NE Greenland) between 24 July and 2 August 2001. This animal was tracked as no. 6481 in 1999 (Table 10.1, Fig. 10.2). Locations were received until 3 September but only locations until 2 August remained after filtering (see Materials and methods).

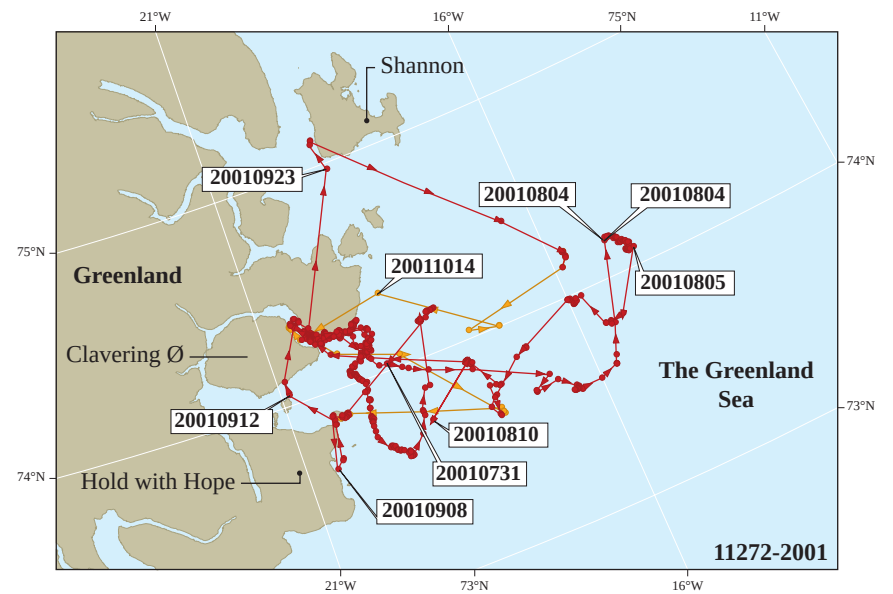

Figure 10.4 Movement of an adult male walrus (no. 11272) in Young Sound and adjacent areas in NE Greenland between 27 July and 14 October 2001. Red tracks = locations received during the open-water period until 3 October when a dense layer of fast ice had formed west of Sandøen. Orange tracks = locations received after formation of fast ice.

Overall, the locations indicated that the four walruses spent a weighted average of about 44% of the time in the Young Sound study area (Table 10.2). When at sea inside Young Sound, the locations indicated a clear preference for the areas in northern parts of the fjord where the waters are shallow (Figs. 10.2 & Fig. 10.5).

10.3.4 Haul-out and diving activity

During the open-water period the four walruses hauled out between c. 21 and 66% of the time. Overall, haul-out time averaged 31.4% (Table 10.3). In total, the walruses spent between c. 11 and 45% of the time in the water inside the study area (Table 10.2). 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 10.2).

Data on diving activity during the open-water season was only available for animal no. 6481/4344. For both years and all months combined, an average of c. 32% of the time at sea was spent between 0 and 6 m depth (about 11% of this time was spent at the surface; i.e. SWS dry), and the remainder of the time was at depths below 6 m (Table 10.4). Less than 1% of the time was spent at depths below c. 40 m.

About 80% of all dives inshore went to depths

Table 10.3 Estimates of haul-out time (%) for four seasons by three adult male walruses during time spent inshore in the Young Sound area (NE Greenland) in 1999 and 2001.

ID no.	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 10.4 Time (%) spent in different depth intervals (TAD, Time-At-Depth) by an adult male walrus (same individual in both years) inshore in the Young Sound area (NE Greenland) in 1999 and 2001.

ID no.	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 saltwater switch was dry
[2)] Includes time at surface.

Table 10.5 Number of dives and percentage of dives made to different depth intervals by an adult male walrus (same individual in both years) inshore in the Young Sound area (NE Greenland) in 1999 and 2001.

ID no.	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)] Haul-out periods excluded

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 10.5). Less than 1% of the dives went deeper than c. 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 made by no. 6481/4344 lasted between 5 and 7 min (c. 77% of all dives were between 4 and 8 min in duration), Table 10.6. 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 lasted more than 8 min.

On days when no. 6481/4344 was inshore, the daily maximum depth readings averaged 35.4 m in 1999 (sd = 24.6, range: 14 – 86 m, n = 7 days with maximum dive depth data), and 26.5 m in 2001 (sd = 7.1, range: 20 – 36 m, n = 8), which is in accordance with direct observations (S. Rysgaard & G. 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 no. 6481/4344 dived to a maximum depth of 136 m on 30 August 1999 at 74˚40´ N and 18˚ 34´ W (i.e. outside Young Sound).

Table 10.6 Number of dives and percentage of dives made in different intervals of dive duration by an adult male walrus (same individual in both years) inshore in the Young Sound area (NE Greenland) in 1999 and 2001.

ID no.	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	115	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)] Haul-out periods excluded

Table 10.7 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 spent about 30% of the time inshore for a total of 1620 ”walrus feeding days”.

	Parameter	Mean/estimated value	95% CI	Comments
A	Number of 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 number of walruses	60	-	Genetically identified (cf. Materials and methods)
E	Walrus feeding days	1620	-	Duration of open-water season, 90 d, *% occupancy * 60 walrus
F	Number of dives/day	118–181	-	Based on Tables 10.5 & 10.6
G	Total number of bivalves eaten	$10.2 * 10^6$–15.6×10^6	-	(A * E * F)
H	Total DM eaten ($\times 10^3$ kg)	28.5–43.7	-	(B * E * F)
I	Total WW eaten ($\times 10^3$ kg)	111–171	-	(C * E * F)
J	Total WW eaten ($\times 10^3$ 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

10.3.5 The number of walruses in Young Sound

The number of animals hauled 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 of 2001–2004 the occurrence on Sandøen of females and young became more frequent (Born et al., 1997; Born et al., 2000; E. W. Born, unpublished data).

Opportunistic and systematic observations (Born & Berg, 1999; E. W. Born, unpublished 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 60. The highest numbers were recorded in 1991 (47), 1994 (48) and 2004 (60) (Born et al., 1997; Born & Berg, 1999; M. Acquarone, unpublished data). The maximum numbers seen on one occasion in the period late July through August 1998–2004 varied markedly (1998: 28, 1999: 9, 2000: 22, 2001: 19, 2002: 19, 2003: 37, 2004: 60; Born & Berg, 1999; Born et al., 2000; Acquarone et al., 2001; M. Acquarone, unpublished data). In 1999, when the lowest number was observed, unusually much pack ice entered Young Sound from the Greenland Sea. Sometimes this ice blocked the beach at the walrus haul-out, probably precluding access to the area. However, during all seasons it was clear from observations of individually recognizable animals (cf. Born et al. 1997) 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 to 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 & E. W. Born, unpublished data).

10.3.6 Average TBM of walruses in Young Sound

Based on photos of 27 male walruses 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.

10.3.7 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 10.7).

Method I

Based on the estimates of the daily mean number of dives to 6 m and deeper, and number of dives lasting between 5 and 7 min, the walruses make a total of c. 191×10^3 to 293×10^3 feeding dives in Young Sound between Sandøen and Zackenberg during the open-water season.

Using the estimates on number of bivalves – SF dry matter and wet weight – consumed per feeding dive (Table 10.7), the estimates (two methods of determining number of feeding dives, Tables 10.5 and 10.6) of the total number of bivalves consumed inshore in Young Sound during the open-water season ranged from ca. 10×10^6 to ca. 16×10^6 (Table 10.7). The estimate of the corresponding amounts of bivalve DM was c. 29 to 44 tons while WW amounted to c. 111 to 171 tons, respectively (Table 10.7).

Method II

The daily mean gross food consumption was c. 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 equaled c. 97 tons (i.e. c. 25 tons DM) (Table 10.7).

10.3.8 Estimation of the impact of walrus predation on the bivalves

Daily feeding rates in walruses of 6% 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. An estimate of the total consumption by walruses during the open-water season of ca. 100 tons wet matter (i.e. 111 and 97

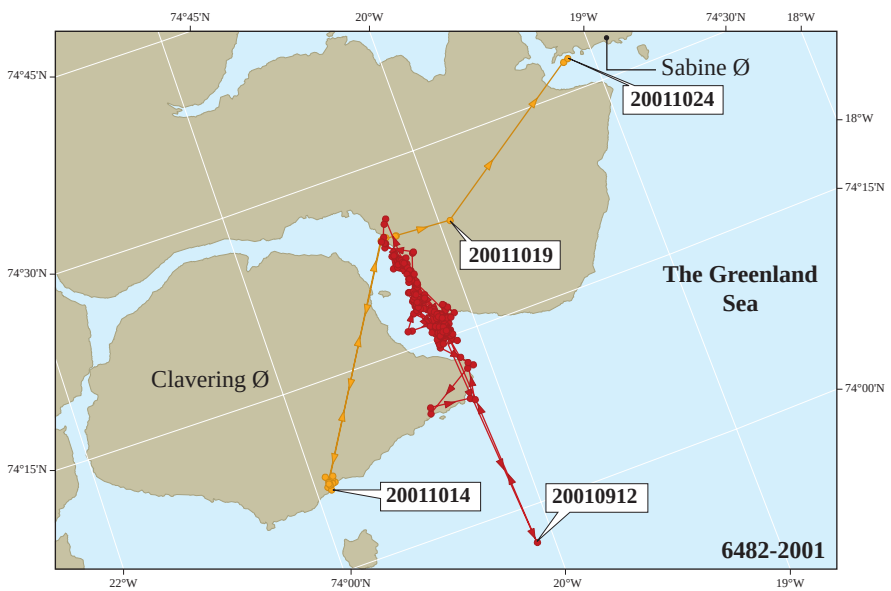

Figure 10.5 Movement of an adult male walrus (no. 6482) in Young Sound and adjacent areas in NE Greenland between 28 July and 24 October 2001. Red tracks = locations received during the open-water period until 6 October when a dense layer of fast ice had formed west of Sandøen. Orange tracks = locations received after formation of fast ice.

Photo: Erik W. Born

An adult male walrus fitted with a ST-10 satellite transmitter monitoring walrus activity in Young Sound.

tons, respectively; Table 10.7, I and J) corresponds to the removal of c. 1.96 g/m^2 SF bivalve WW down to 60 m depth in the areas of Young Sound (total area: 50.96 km^2) that we extrapolate to.

The standing biomass and annual production down to 60 m depth of the two important walrus food items *Mya* sp. and *Hiatella* sp. were determined in the areas between Sandøen and the Basalt Ø (biomass and production of *Serripes* sp. were not determined). In that area (24.13 km^2, <60 m depth), the SF WW biomass and annual production of *Mya* and *Hiatella* taken together are c. 78 g m^{-2} yr^{-1} and 7.9 g m^{-2} yr^{-1} × year, respectively (Chapter 7). Hence, our estimate of walrus predation per m^2 amounts to c. 2.5% of the standing biomass of *Mya* sp. and *Hiatella* sp., and c. 25% of the annual production of these bivalves. However, one must keep in mind that in Young Sound the walruses also forage on other bivalves and benthic invertebrates (Born et al., 1997, 2003).

10.4 Discussion

10.4.1 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 & Born, 1994). This indicates that the average TBM used in the present study is reasonable.

10.4.2 Movement

The area of interest to the multi-disciplinary study of marine productivity has been defined as being the areas between Sandøen and Basalt Ø in particular (Chapter 11). 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 has been calculated (Chapter 11). However, the general scarcity of "at sea" locations received from the walruses tracked in the present study only allowed determination of time in Young Sound west of Sandøen to Zackenberg and not sub-division of the time budget in this area.

The satellite-derived locations 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 of Zackenberg. However, during the study period, the animals also used other feeding locations south, east and north of Young Sound. The latter area (i.e. the Sabine Ø–Lille Pen-

dulum 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 c. 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 hauled out walrusses is relatively high, whereas fewer locations, usually of lower precision, are received from animals 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 (E.W. Born, unpubl. data), resulting in no or too 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.

10.4.3 Haul-out and diving activity

We tracked relatively few animals during two open-water seasons. However, the activity of the animals 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 deeper than 6 m as feeding dives. The proportions of the number of dives to these depths were within the range observed in walruses studied in Dove Bay in August 2001. Here, 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 to >6 m/24 "wet" h (range: 108–208 dives/24 h) (Acquarone, 2004).

Visual observations of walruses feeding along the northern coast of Young Sound indicate that they feed between c. 8 and 34 m (Born et al., 2003). The vast majority of dives were between 6 and 42 m, which is typical of walruses that are thought 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 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 water. If "at surface" intervals of c. 1 min between feeding dives (Born & Knutsen, 1997; Born et al., 2003) are added it follows that the walruses were engaged in diving for food for between 57% ("dive duration") and 88% ("dives at depth") of their "in water" time. Six adult male walruses 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 recorders 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 a reasonable approach.

However, some dives deeper than 6 m and 5–7 min long could have been unsuccessful feeding dives. If so, the amount of food consumed by the walruses is overestimated to an unknown extent.

10.4.4 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 and 2004 were years with very little ice in the area probably caused the walruses to use Sandøen intensively as a haul-out. Consequently, many walruses used the haul-out during those years, 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. In August 2001, Levermann et al. (2004) studied walrus foraging activity through direct observations

Photo: Göran Ehlmé.

As part of this study, walrus feeding during individual dives was determined by collecting shells of recently predated bivalves (c.f. Born et al. 2003).

within a 1.5-km^2 area at the coast c. 5 km north of the island Sandøen. They found that the probability of a walrus being present within the observation area at any given time was 0.47. Hence, provided that the walrus activity in the observation area of Levermann et al. (2004) 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 ($[51/1.5] \times 0.47$).

We estimated that the average TBM of the walruses in Young Sound is about 1000 kg. This is somewhat higher than the 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) assumed that the daily food consumption of a 1000 kg walrus is 5.7%. Measurement of walrus energy expenditure by use of double-labeled water in NE Greenland in 2001 indicated that daily gross food consumption in adult male walruses is 5–6% of TBM (Acquarone, 2004). Fay (1982) estimated that daily food intake in free-ranging walruses is 4–8% of TBM. 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 c. 2.5 tons of bivalve SF wet matter was removed in the 1.5-km^2 observation area (ca. 1.67 g/m^2 SF bivalve WW) during the 90-day open-water period. If we apply this estimate to the total foraging area used in the present study, walruses may consume an estimated c. 85 tons of clam meat in Young Sound during the open-water season. However, in Levermann et al. (2004) the study area constituted only c. 3% of the outer region of the fjord and covered a smaller part of the inshore period.

10.4.5 The impact of the walruses on the bivalve community

A high standing stock of bivalves is present in the study area (Sejr et al., 2000; Sejr et al., 2002; Chapter 7), 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).

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 considered as well, the inshore bivalve banks in Young Sound represent a richer food source than accounted for in our calculation of predation, which is based on only 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) and were based on three bivalve species that constitute the far most important portion of the walrus diet. However, walruses feed on a variety of benthic food (e.g. Fay, 1982) and as pointed

out by Born et al. (2003) it is not unlikely that walruses in Young Sound may also feed on other bivalves (e.g. *Astarte* sp.) and invertebrate benthos (*e.g*. polychaetes, sea cucumbers and gastropods) besides 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) as well as being 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 indicate that walrus predation in Young Sound is below the carrying capacity of this fjord. This latter conclusion is supported by the fact that, historically, walruses were more abundant in the area (Born et al., 1997).

10.5 Acknowledgments

This study was supported financially by The Danish Natural Science Research Council, The Commission for Scientific Research in Greenland (KVUG), The Greenland Institute of Natural Resources (GN) and The Danish National Environmental Research Institute (NERI). Special thanks to Søren Rysgaard and Mikael Sejr (NERI, Silkeborg, Denmark), Liselotte W. Andersen (NERI, Kalø, Denmark), Göran Ehlmé (WaterProof, Partille, Sweden), Nette Levermann (GN, Nuuk, Greenland), Lars Heilmann (GN) and Lars Ø. Knutsen (Cinenature, Löa, Sweden) for inspiring co-operation in the field and during various phases of analyses. Also thanks to David Griffiths (The Norwegian School of Veterinary Science, Oslo, Norway), Torsten Møller (Kolmården Zoological Garden, Kolmården, Sweden), the Danish Military Patrol, Sirius in Northeast Greenland, and the Danish Polar Centre for valuable support during this study. We thank Wildlife Computers (Seattle, USA) for their enthusiastic work on developing the satellite tags for walrus, and Christina Lockyer (Age-Dynamics, Lyngby, Denmark) for ageing walrus no. 6482. R.E.A. Stewart (Department of Fisheries and Oceans, Winnipeg, Canada) and Ian Gjertz (The Research Council of Norway), who acted as referees on the paper, are thanked for offering useful comments that greatly improved it. We also wish to thank Søren Rysgaard and Ronnie Glud for offering comments that improved the paper.

10.6 References

Acquarone, M. 2004. Body composition, field metabolic rate and feeding ecology of walrus (*Odobenus rosmarus*) in Northeast Greenland. PhD Thesis. National Environmental Research Institute and University of Veterinary Science, Denmark, 142 pp.

Acquarone, M., Born, E. W. & Griffiths, D. 2001. Studies of walrus energetics and behaviour. In: Caning, K & Rasch, M. (eds.). Zero Zackenberg Ecological Research Operations 6th Annual Report. Danish Polar Center, Ministry of Research and Information Technology, Copenhagen, Denmark, 80 pp.

Andersen, L. W., Born E. W., Gjertz, I., Wiig, Ø., Holm, L. E. & Bendixen, C. 1998. Population structure and gene flow of the Atlantic walrus (*Odobenus rosmarus rosmarus*) in the eastern Atlantic Arctic based on mitochondrial DNA and microsatellite variation. Mol. Ecol. 7: 1323-1336.

Born. E. W. & Knutsen, L. Ø. 1990a. Immobilization of Atlantic walrus (*Odobenus rosmarus rosmarus*) by use of etorphine hydrochloride reversed by diprenorphine hydrochloride. Technical Report No. 14. Greenland Home Rule. Department of Wildlife Management, Nuuk, Greenland: 1-15.

Born, E. W. & Knutsen, L. Ø. 1990b. Satellite tracking and behavioural observations of Atlantic walrus (*Odobenus rosmarus rosmarus*) in NE Greenland in 1989. Technical Report No. 20. Greenland Home Rule. Department of Wildlife Management, Nuuk, Greenland: 1-68.

Born, E. W. & Knutsen, L. Ø. 1992. Satellite-linked radio tracking of Atlantic walruses (*Odobenus rosmarus rosmarus*) in northeastern Greenland. Z. Saügetierk 57: 275-287.

Born, E. W., Gjertz, I. & Reeves, R. R. 1995. Population assessment of Atlantic walrus (*Odobenus rosmarus rosmarus*). Nor. Polarinst. Medd. 138: 1-100.

Born, E. W. & Knutsen, L. Ø. 1997. Haul-out activity of male Atlantic walruses (*Odobenus rosmarus rosmarus*) in northeastern Greenland. J. Zool. (Lond.) 243: 381-396.

Born, E. W., Dietz, R., Heide-Jørgensen, M. P. & Knutsen, L. Ø. 1997. Historical and present status of the Atlantic walrus (*Odobenus rosmarus rosmarus*) in eastern Greenland. Meddr. Grønland., Biosci. 46: 1-73.

Born, E. W. & Berg, T. B. 1999. A photographic survey of walruses (*Odobenus rosmarus*) at the Sandøen haul-out (Young Sound, eastern Greenland) in 1998. Technical Report no. 26. Greenland Institute of Natural Resources, Nuuk: 1-19.

Born, E. W., Acquarone, M. & Griffiths, D. 2000. Studies of walrus energetics and behaviour. In: Zero Zackenberg Ecological Research Operations 5th Annual Report. Danish Polar Center, Ministry of Research and Information Technology, Copenhagen, Denmark: 72-73.

Born, E. W., Andersen, L. W., Gjertz, I. & Wiig, Ø. 2001. A review of genetic relationships of Atlantic walruses (*Odobenus rosmarus rosmarus*) east and west of Greenland. Polar Biol. 24 (10): 713-718.

Born, E. W., Teilmann, J. & Riget, F. 2002. Haul-out activity of ringed seals (*Phoca hispida*) determined from satellite telemetry. Mar. Mamm. Sci. 18(1): 167-181

Born, E. W. Rysgaard, R., Ehlmé, G., Sejr, M. K., Acquarone, M. & Levermann, N. 2003. Underwater observations of foraging free-living walruses (*Odobenus rosmarus*) including estimates of their food consumption. Polar. Biol. 26: 348-357.

Berthelsen, E. 1937. Contributions to the animal ecology of the fiords of Angmagssalik and Kangerlugssuaq in East Greenland. Meddr. Grønland. 108(3), 58 pp.

Comiso, J. C. 2002. A rapidly declining perennial sea ice cover in the Arctic. Geophys. Res. Lett. 29: 1956.

Comiso, J. C. & Parkinson, C. L. 2004: Satellite-observed changes in the Arctic. Physics Today, August 2004: 38-44.

Fay, F. H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. U.S. Department of the Interior Fish and Wildlife Service. North American Fauna 74: 1-279.

Fay, F. H., Bukhtiarov, Y. A., Stoker, S. W. & Shults, L. M. 1984. Foods of the Pacific walrus in winter and spring in the Bering Sea. In: Fay F. H. & Fedoseev, G. A. (eds.). Soviet-American Cooperative Research on Marine Mammals. Vol. 1 - Pinnipeds. NOAA Technical Reports NMFS 12. Washington D.C., USA: 81-88.

Førland, E. J., Hanssen-Bauer, I., Jónsson, T., Kern-Hansen, C., Nordli, P. Ø., Tveito, O. E. & Vaarby Laursen, E. 2002. Twentieth-century variations in temperature and precipitation in the Nordic Arctic. Polar. Rec. 38(206): 203-210.

Gjertz, I., Griffiths, D., Krafft, B. A., Lydersen, C. & Wiig, Ø. 2001. Diving and haul-out patterns of walruses *Odobenus rosmarus* on Svalbard. Polar. Biol. 24: 314-319.

Griffiths, D., Wiig, Ø., Gjertz, I. 1993. Immobilization of walrus with etorphine HCl hydrochloride and Zoletil®. Mar. Mamm. Sci. 9: 250-257.

Grebmeier, J. M., Feder, H. M. & McRoy, P. 1989. Pelagic-benthic coupling on the shelf of the northern Bering and Chuckchi Seas. II. Benthic community structure. Mar. Ecol. Prog. Ser. 51: 253-268.

Hanssen-Bauer, I. 2002. Temperature and precipitation in Svalbard 1912-2050: measurements and scenarios. Polar. Rec. 38(206): 225-232.

Harris, R. B., Fancy, S. G., Douglas, D. C., Garner, G. W., Amstrup, S. C., McCabe, T. R. & Pank, L. F. 1990. Tracking wildlife by satellite: current systems and performance. United States Department of the interior fish and wildlife service, Washington, D.C., USA: 1-52.

Hills, S. 1992. The effect of spatial and temporal variability on population assessment of Pacific walruses. PhD-thesis, University of Maine, Orono, U.S.A.

Jay, C., Farley, S. D. & Garner, G. W. 2001. Summer diving behaviour of male walruses in Bristol Bay, Alaska. Mar. Mam. Sci. 17: 617-631.

Kelly, B.P. 2001. Climate change and ice breeding pinnipeds. In: Walther, G-R., Burga C.A. & Edwards, P.J. (eds.). Fingerprints of climate changes, adapted behaviour and shifting species range. Kluwer Academic/ Plenum Publishers, New York 2001: 43-55.

Knutsen, L. Ø. & Born, E. W. 1994. Body growth in Atlantic walruses (*Odobenus rosmarus rosmarus*) from Greenland. J. Zool. (Lond.) 234: 371-385.

Levermann, N., Sejr, M. K., Rysgaard, S. & Born, E. W. 2004. Walrus foraging ecology and area use in a Northeast Greenlandic fiord. In preparation for Mar Ecol Prog Ser. Chapter II. In: Levermann, N.: Waltzing with walruses. M. Sc. thesis, November 2004, University of Copenhagen: 141 pp.

Loughrey, A. G. 1959. Preliminary investigation of the Atlantic walrus *Odobenus rosmarus rosmarus* (Linnaeus). Can. Wildl. Serv., Wildl. Manage. Bull. Ser. 1 No. 14: 123 pp.

Mansfield, A. W. 1958. The biology of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus) in the eastern Canadian arctic. Fisheries Research Board of Canada Manuscr. Rep. Ser. (Biol.) No. 653: 1-146.

Ockelmann, K. 1958. Marine Lamellibranchiata. Meddr. Grønland. 122(4), 256 pp.

Oliver, J. S., Slattery, P. N., O´Connor, E. F. & Lowry, L. F. 1983. Walrus, *Odobenus rosmarus*, feeding in the Bering Sea; a benthic perspective. Fish. Bull. 81: 501-512.

Parkinson, C. L. 1992. Spatial patterns of increases and decreases in the length of the sea ice season in the North Polar Region, 1979-1986. J. Geophys. Res. 97: 14377-14388.

Parkinson, C. L. 2000. Variability of Arctic Sea ice: The view from the space, an 18-year record. Arctic 53: 341-358.

Payer, J. 1877a. Upptäcktsresor i Norra Polarhafvet [Discoveries in the northern Polar Sea]. Albert Bonniers Förlag, Stockholm (In Swedish).

Payer, J. 1877b. Den østrisk-ungarnske Nordpol-Ekspedition i Aarene 1872-1874 [The Austrian-Hungarian North Pole Expedition in the Years 1872-1874]. København (In Danish).

Peters, W. 1874. Die zweite deutsche Nordpolfärht in den Jahren 1869 und 1870 unter Führung des Kapitän Karl Koldewey [The second German North Pole Expedition in the Years 1869 and 1870 under the Command of Captain Karl Koldewey]. F.A. Brockhaus, Leipzig (In German).

Rothrock, D. A., Yu, Y. & Maykut, G. A. 1999. Thinning of the Arctic sea-ice cover. Geophys. Res. Lett. 26: 3469-3472.

Rysgaard, S., Dahlgaard, H. & Finster, K.1996. Primary production, nutrient dynamics and mineralization in a northeastern Greenland fjord during the summer thaw. Polar. Biol. 16: 497-506.

Rysgaard, S., Thamdrup, B., Risgaard-Petersen, N., Fossing, H., Berg, P., Christensen, P. B. & Dalsgaard, T. 1998. Seasonal carbon and nitrogen mineralization in a high-Arctic coastal marine sediment, Young Sound, Northeast Greenland. Mar. Ecol. Prog. Ser. 175: 261-276.

Rysgaard, S., Nielsen, T. G. & Hansen, B. 1999. Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. Mar. Ecol. Prog. Ser. 179: 13-25.

Rysgaard, S., Vang, T., Stjernholm, M., Rasmussen, B., Windelin, A. & Kiilsholm, S. 2003. Physical conditions, carbon transport and climate change impacts in a NE Greenland fjord. Arct. Antarct. Alp. Res. 35(3): 301-312.

Rysgaard, S., Frandsen, E., Sejr, M. K., Dalsgaard, T., Blicher, M. E. & Christensen, P. B. 2005. Zackenberg Basic: The MarineBasic Programme. In: Rasch, M & Caning, K. (eds.) Zackenberg Ecological Research Operations, 10th Annual report, 2004. Danish Polar Center, Ministry of Science, Technology and Innovation. Copenhagen. 85 pp.

Sejr, M. K., Jensen, K. T. & Rysgaard, S. 2000. Macrozoobenthos in a Northeast Greenland Fjord: Structure and Diversity. Polar Biol. 23: 792-801.

Sejr, M. K., Sand, M. K., Jensen, K. T., Petersen, J. K., Christensen, P. B. & Rysgaard, S. 2002. Growth and production of *Hiatella arctica* (Bivalvia) in a high-arctic fjord (Young Sound Northeast Greenland) Mar. Ecol. Prog. Ser. 244: 163-169.

Sejr, M. K. 2002. Functional importance of macrozoobenthos in Young Sound, NE Greenland. PhD-thesis, University of Aarhus, Denmark, 159 pp.

Sheffield, G., Fay, F. H., Feder, H. & Kelly, B. P. 2001. Laboratory digestion of prey and interpretation of walrus stomach contents. Mar. Mamm. Sci. 17: 310-330.

Thomson, D. H., Martin, C. M. & Cross, W. E. 1986. Identification and characterization of arctic nearshore benthic habitats. Technical Report 1434. Can. Fish. Aquat. Sci., 70 pp.

Vibe, C. 1950. The marine mammals and the marine fauna in the Thule district (Northwest Greenland) with observations on the ice conditions in 1939-41. Meddr. Grønland. 150, 115 pp.

Welch, H. E., Bergmann, M. A., Siferd, T. D., Martin, K. A., Curtis, M. F., Crawford, R. E., Conover, R. J. & Hop, H. 1992. Energy flow through the marine ecosystem of the Lancaster Sound region, Arctic Canada. Arctic 45: 343-357.

Wiig, Ø., Gjertz, I., Griffiths, D. & Lydersen, C. 1992. Diving patterns of an Atlantic walrus *Odobenus rosmarus rosmarus* near Svalbard. Polar. Biol. 13: 71-72.

Wiig, Ø., Gjertz, I. & Griffiths, D. 1996. Migration of walruses (*Odobenus rosmarus*) in the Svalbard and Franz Josef Land area. J. Zool. (Lond.) 238: 769-784.

Witting, L. & Born, E. W. 2005. An assessment of Greenland walrus populations. ICES J. Mar. Sci. 62: 266-284.