An assessment of the effects of hunting and climate on walruses in Greenland

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2005

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Summary

The present status of Atlantic walruses (*Odobenus rosmarus rosmarus*) in Greenland is reviewed in relation to historical exploitation and the carrying capacity of their food resources. The relative effects of exploitation and climate change on the walrus populations are assessed, and speculative projections are made concerning the fate of walruses in a warming Arctic in view of the species' evolutionary history.

The present distribution of walruses in Greenland is governed by (1) the restricted distribution of critical habitats (foraging areas, wintering sites, terrestrial haul-outs), and (2) past and present hunting patterns of foreign and Greenland hunters. Various studies, including genetic analyses and satellite-telemetry, have shown that three different sub-populations or stocks occur in Greenland waters: (1) West Greenland sub-population, (2) North Water sub-population inhabiting Northwest Greenland and the eastern Canadian High Arctic, and (3) East Greenland sub-population. There is little interchange among the three sub-populations and hence their status must be evaluated separately.

Several life history traits of walruses, in particular their gregariousness and fidelity to localized near-shore areas, make them particularly vulnerable to modern hunting involving the use of motorized vessels and firearms.

In West Greenland, a marked change in patterns of exploitation of marine resources driven by climatic and socio-economic factors led to an increased catch of walruses during the first half of the 20th century. In Northwest Greenland, the widespread use of motorized vessels did not begin until the 1960s. Between 1889 and the 1950s foreign sealers and trappers took a heavy toll on walruses in East Greenland. During a brief period in the mid-1920s, walruses were important game animals for the Inuit living at the entrance to Scoresby Sound in East Greenland.

Recent estimates of the total numbers of walruses in the sub-populations exploited in Greenland are: West Greenland ca. 1000 animals, North Water ca. 1500, and East Greenland ca. 1000. Modeling indicates that the West Greenland and North Water sub-populations were over-exploited during the 20th century and that their present abundance is far below their historical abundance. Apparently, both of these sub-populations are still being exploited above sustainable levels. After protective measures were introduced in the 1950s, the East Greenland sub-population, which has its main distribution in the "National Park of North and Northeast Greenland", likely increased to close to its pre-exploitation abundance, and the present exploitation appears to be sustainable.

Estimates of the amount of food for walruses in Central West Greenland and in the North Water indicate that in these areas the number of walruses is far below the carrying capacity level. Insufficient information on bathymetry did not allow for a similar evaluation for East Greenland. However, recent studies indicate that walrus food is still abundant there, at least locally.

During their long evolutionary history, walruses have experienced extremes of both warming and cooling. Climate and ice conditions around Greenland were severe during the first half of the 19th century, but temperatures have increased thereafter. Both East and West Greenland experienced a warm period with relatively light ice conditions from the 1920s until the 1960s, followed by cooling with an associated increase in sea ice, until ca. 1990. Since the early 1990s temperatures have increased markedly, resulting in a reduction in sea ice in East Greenland and, more recently, in the Davis Strait region.

Walruses, in contrast to other pagophilic marine mammals like polar bears, *Ursus maritimus*, and ringed seals, *Pusa hispida*, probably will be able to cope with future warmer conditions in the Arctic. Walrus-type precursors evolved during the Miocene in ice-free waters of the Northern Hemisphere. Prior to the Pliocene-Pleistocene

glaciations beginning about 2.5 Ma B.P. (i.e. million years before present), walruses (or their immediate ancestors) had become highly specialized suction-feeders on benthic invertebrate prey. Their use of terrestrial haul-outs, and the fact that they have morphological modifications (pharyngeal pouches) that allow them to cope with situations where there is no ice for hauling out, probably reflect their early evolution in warmer waters. These traits will probably also enable them to cope with a future with less or no ice. Historically walruses occurred, and they still do occur, year-round in ice-free waters at low latitudes.

A cooling event ca. 2 Ma B.P. exterminated a major part of the mollusks at lower latitudes within the range occupied by walruses. As a consequence of this habitat degradation, walruses were confined to cooler areas in the north where cold-resistant mollusks survived. Glaciations of the Northern Hemisphere forced walruses to live at the margin of the ice sheet. During this reduction in extent of their habitat, walruses had to adapt to temperate-Arctic conditions. During the last de-glaciation, they expanded their range northward. Their present Arctic distribution likely reflects the fact that exploitation by humans simply exterminated walruses in more temperate latitudes.

It is concluded that (1) exploitation by man has been the main driving force behind the dynamics (and severe reduction) in Greenland walrus sub-populations, (2) warming during the 20th century reduced the extent of sea ice and increased the accessibility of walruses to hunters, leading to increased exploitation in Greenland, (3) walruses may ultimately benefit from warming and a consequent reduction in sea ice, and (4) the future "warm" scenario in Greenland, with a greater dependence of walruses on terrestrial haul-outs, and their increased accessibility to human hunters and polar bears, signals a need for strict regulation of walrus hunting in Greenland.

Contents

List of papers

Paper 1   Born, E.W. & L.Ø. Knutsen 1992. Satellite-linked radio tracking of Atlantic walruses (*Odobenus rosmarus rosmarus*) in northeastern Greenland, 1989-1991. *Zeitschrift für Säugetierkunde* 57: 275-287.

Paper 2   Born, E.W. & I. Gjertz 1993. A link between walruses (*Odobenus rosmarus*) in northeast Greenland and Svalbard. *Polar Record* 29 (171): 329.

Paper 3   Born, E.W., M.P. Heide-Jørgensen & R.A. Davis 1994. The Atlantic walrus (*Odobenus rosmarus rosmarus*) in West Greenland. *Meddelelser om Grønland, Bioscience* 40: 1-33.

Paper 4   Knutsen, L.Ø. & E.W. Born 1994. Body growth in Atlantic walruses (*Odobenus rosmarus rosmarus*) from Greenland. *Journal of Zoology (London)* 234: 371-385.

Paper 5   Born, E.W. & L.Ø. Knutsen 1997. Haul-out activity of male Atlantic walruses (*Odobenus rosmarus rosmarus*) in northeastern Greenland. *Journal of Zoology (London)* 243: 381-396.

Paper 6   Born, E.W., R. Dietz, M.P. Heide-Jørgensen & L.Ø. Knutsen 1997. Historical and present status of the Atlantic walrus (*Odobenus rosmarus rosmarus*) in eastern Greenland. *Meddelelser om Grønland, Bioscience* 46: 1-73.

Paper 7   Born, E.W. 2001. Reproduction in female Atlantic walruses (*Odobenus rosmarus rosmarus*) from northwestern Greenland. *Journal of Zoology (London)* 255: 165-174.

Paper 8   Born, E.W., L.W. Andersen, I. Gjertz & Ø. Wiig 2001. A review of the genetic relationships of Atlantic walruses (*Odobenus rosmarus rosmarus*) east and west of Greenland. *Polar Biology* 24 (10): 713-718.

Paper 9   Born, E.W., S. Rysgaard, G. Ehlmé, M. Sejr, M. Acquarone & N. Levermann 2003. Underwater observations of foraging free-living walruses (*Odobenus rosmarus*) including estimates of their food consumption. *Polar Biology* 26: 348-357.

Paper 10 Born, E.W. 2003. Reproduction in male Atlantic walruses (*Odobenus rosmarus rosmarus*) from the North Water (N Baffin Bay). *Marine Mammal Science* 19(4): 819-831.

Paper 11 Born E.W. & M. Acquarone 2005. An estimation of walrus predation on bivalves in the Young Sound area (NE Greenland). *In:* Rysgaard, S. & R.N. Glud (eds.). Carbon cycling in Arctic marine ecosystems: Case study – Young Sound. *Meddelelser om Grønland, Bioscience*. In press.

Paper 12 Witting, L. & E.W. Born 2005. An assessment of Greenland walrus populations. *ICES Journal of Marine Science* 62: 266-284.

Paper 13 Born, E.W., M. Acquarone, L.Ø. Knutsen & L. Toudal 2005. Homing behaviour in an Atlantic Walrus (*Odobenus rosmarus rosmarus*). *Aquatic Mammals* 31(1): 11-21.

Introduction

Most people think they know the walrus, at least from cartoon images – an animal with a stiff moustache and red, ill-tempered eyes; a big, somewhat clumsy beast that may not be very intelligent. But few people living today have seen walruses in their proper, real-life setting because the animals live in the remoter reaches of the Arctic. Becoming acquainted with walruses as elements within a natural ecosystem is not easy.

The walrus (*Odobenus rosmarus*) is a member of the Carnivora and of a group of marine mammals informally known as pinnipeds, or fin-footed ones. Its closest living relatives are the sea lions (Otariidae). As a distinctly social animal, with limited dispersal abilities and rather rigid habitat requirements, the walrus is vulnerable to exploitation. Throughout its range the Atlantic walrus (*O.r. rosmarus* Linnaeus, 1758) was heavily exploited by European whalers and sealers, causing major reductions in its extent of occurrence and in its numbers. Atlantic walruses are still hunted by residents of Greenland and Canada. In nearly all areas, including Greenland, Atlantic walruses apparently remain well below their historical levels of abundance (Born et al. 1995).

As noted above, walruses are not easy to study. Their total range in West, Northwest and East Greenland spans roughly 260000 km^2. For the most part, these creatures live in areas that are difficult to reach and inhospitable. In West Greenland they occur in the offshore pack ice during winter and spring. In Northwest Greenland (i.e. in the North Water polynya) walruses stay offshore in the dense ice during spring and fall, whereas during winter they come closer to shore but remain in areas covered with thin and unstable ice. On the eastern coast of Greenland they are distributed mainly inside the border of the unpopulated "National Park of North and Northeast Greenland". When Atlantic walruses are killed by hunters in Greenland and Canada, they are usually butchered in the drifting pack ice. Therefore, biological samples are difficult to obtain, and this limits what can be learned about the biology of Atlantic walruses. Nevertheless, studies over a number of years have allowed colleagues and I to gain some insights into the biology of walruses in Greenland, to estimate their abundance and to assess the nature and scale of removals by hunting. When taken together, the available information is sufficient to allow an evaluation of the status of walruses in Greenland.

During the last few decades the Arctic has become a warmer place to live (e.g. Hassol 2004) and it has been suggested that warming negatively affects walruses (Kelly 2001; Hassol 2004). During their long evolutionary history, walruses and their precursors have experienced both warm and very cold periods. The latest period of warming in Greenland lasted from ca. 1920 until ca. 1960.

Clearly, temperature and ice regimes influence Arctic marine mammals, including walruses. It therefore seems that an evaluation of the present status of walruses in Greenland should focus on the relative importance of two main driving factors: exploitation by man and climatic fluctuations. The following questions can be posed:

(i)   How has exploitation affected walruses in Greenland?
(ii) What were the effects of past climatic fluctuations on the population?
(iii) What was the relative importance to the walrus population of exploitation and climate change?
(iv) How might these factors affect walruses in the future?

Structure of the thesis

The thesis consists of a "General introduction, discussion and conclusion" chapter and 13 scientific papers. First I review the findings of the papers and their significance for the evaluation of the status of walruses in Greenland followed by the general introduction which is divided into two parts.

The first part of the thesis summarizes (1) systematics and taxonomy, (2) important life history traits of walruses, (3) the physical environment of "walrus areas" in Greenland, (4) evidence for population substructure, distribution and abundance, (5) socio-economic developments in Greenland in the 20th century (e.g. an increase in the population of Greenlanders, the use of modern hunting technologies) and (6) the magnitude of catches and their impacts on the sub-populations.

The second part evaluates (1) the trophic role of walruses and food requirements, (2) the status of walruses in Greenland in relation to the carrying capacity of their food resources, (3) climate changes during the last few centuries and predicted future weather and ice conditions, and (4) the capacity of Atlantic walruses to survive in warmer conditions.

I suspected that the walrus basically is a "warm water" species that, through bio-geographical circumstances, has become isolated in the Arctic. To explore this thesis, I reviewed the literature on the species' evolution. While doing so, however, I found myself drawn into the details of the fascinating story about the "making of walruses". In order not to tire the reader with excessive details or detract from the thesis itself, I have relegated my summary and interpretation of that story to an appendix on the evolution and zoogeography of walruses and the mollusks to which they are ecologically tied.

The overall findings in the papers and their significance

The papers in the thesis cover a range of studies in various fields of biology. Several of the studies have provided basic knowledge concerning the behavior and biology of Atlantic walruses, and much of this information is applicable to walruses in other parts of their range. All of the studies have focused on providing information necessary to evaluate the historical, present and future status of walruses in Greenland, given their exploitation by humans and

their exposure to fluctuations in climate. Each of the studies addresses one or more of the following topics:

A) Methodology.
B) General behavior (diving and haul-out activity) and movement.
C) Stock identification (delineation of sub-populations).
D) Hunting by humans.
E) Abundance and conservation status.
F) Trophic role and impact of climate change.
G) General biology (vital rates).

In this section the findings of each paper are summarized. By referring to the letter-code given above, I indicate in each case how the study has contributed to answering basic questions of the thesis. Furthermore, in the "General introduction, discussion and conclusion" section, the findings of the papers will be cited by referring to the specific number of the paper in question (see list of papers).

Paper 1 (Topics: A, B, C)

In August 1989 and 1990, a total of 12 adult male Atlantic walruses were immobilized at a haul-out ("Lille Snenæs") in Dove Bay, Northeast Greenland (ca. 76° 52′ N, 19° 38′ W) and a satellite transmitter was attached to a tusk of each. The purposes was to (a) develop a satellite telemetry system that worked with walruses, and (b) determine the movement patterns of individuals. In 1989 contact was maintained for an average of 53 d (SD=36.3; range: 15-111 d; n=6). In 1990, 4 similar transmitters (different antennas) operated for an average of 125 d (SD=96.9; range: 4-238 d; n=6), and 2 transmitters of another type functioned for 62 and 112 days, respectively. During the inshore foraging period (August-September) the walruses used the same haul-out from which they made excursions to a distance of about 80 m from shore. Formation of fast ice in autumn forced the walruses offshore into the Greenland Sea, where they moved north to winter between 80°-82° N (i.e. in the Northeast Water polynya).

Novel findings were (a) walruses in this area used the same foraging grounds each summer, (b) they moved north to winter in the Northeast Water polynya, and (c) gross movements indicated that walruses in Northeast Greenland constitute a separate demographic unit.

Paper 2 (Topics: **B, C**)

In July 1992 a male walrus was photographed at Moffen Island (80° 03′ N, 14° 30′ E) off the northern coast of Spitsbergen (Svalbard archipelago). The photograph showed that it had a numbered tag on its right flipper. The number revealed that the animal had been tagged at the Lille Snenæs haul-out in Northeast Greenland (ca. 76° 52′ N, 19° 38′ W) in August 1989 (animal 33 = 1959 in Paper 1). The same animal had also been observed at Lille Snenæs in August 1990 (no observations in 1991). The study indicated that (a) at least some walruses are capable of moving long distances (700 km) across deep waters, and (b) there is some, but presumably not much, exchange between walruses in Northeast Greenland and Svalbard.

This was the first demonstration of movement of walruses between Greenland and Svalbard.

Paper 3 (Topics: **D, E**)

The historical and present distribution and catch of walruses in West Greenland were reviewed. In the early parts of the 20th century, walruses were abundant off Central West Greenland between ca. 66° N and ca. 70° 45′ N. During autumn, hundreds of walruses used several haul-outs (*uglit*) between ca. 67° 30′ N and ca. 67° 45′ N. From 1911 the hunt at these *uglit* was intensified and by the late 1930s walruses had permanently abandoned them. During 1911-1940 the catch of walruses increased rapidly, reaching a maximum of more than 600 animals reported in 1938 and 1940. A rapid drop in the annual catch followed, apparently reflecting a decrease in the number of walruses wintering in West Greenland. Line-transect aerial surveys conducted in early spring of 1990 and 1991 covered the main wintering grounds between Aasiaat-Sisimiut and the area west

of Disko Island (i.e. ca. 66° 30′ N – ca. 70° 30′ N), resulting in an abundance estimate of ca. 500 walruses (not corrected for submerged animals). The study showed that the number of walruses in West Greenland is much lower today than it was historically, and that walruses in this area are vulnerable to over-exploitation.

The study documented (a) historical and present distribution, (b) present abundance and (c) catches in West Greenland. The data on catch and abundance were used subsequently to model the historical and present status of walruses in West Greenland (Paper 12).

Paper 4 (Topics: **C, F**)

In the years 1977-78 and 1989-91, morpho-metric data were collected from 105 Atlantic walruses in Northwest Greenland (i.e. the North Water polynya). Twenty-one of the animals were subjected to detailed analysis of body composition. The asymptotic standard body length (SL) of walruses from Northwest Greenland was 269 cm for females and 314 cm for males. This is similar to Pacific walruses (*O.r. divergens*), but significantly longer than Atlantic walruses from Hudson Bay in Canada. The asymptotic total body mass (TBM) of walruses in Northwest Greenland was estimated at 720 kg for females and 1114 kg for males. The average walrus consisted of 18% blubber, 12% skin, 12% viscera and 58% blood, muscle and skeleton (muscles were estimated to constitute 44% of TBM).

The study documented (a) differences in growth patterns in Atlantic walruses from different parts of their range and (b) provided data to be used to estimate average TBM in the population and individual walruses in connection with estimates of individual food consumption (Paper 9 and 11).

Paper 5 (Topics: **A, B, E, F**)

In August 1989 and 1990, movements, haul-out and dive activity of male walruses were studied at the "Lille Snenæs" haul-out in Dove Bay, Northeast Greenland (ca. 76° 52′ N, 19° 38′ W). A group of walruses, in-

cluding some that could be individually identified from natural markings, was observed directly. In addition, the activities and movements of 8 adults equipped with satellite transmitters (Paper 1) were monitored during August-September. In both years, instrumented walruses were hauled out ca. 30% of the time. In 1989, when ice floes were available for hauling out, the walruses spent ca. 11% of the time on ice, whereas in 1990, when ice was absent from the study area, they hauled out only on land. The walruses hauled out mainly during the afternoon and evening. Numbers hauling out on land during August was negatively correlated with wind direction, precipitation (rain) and wind-chill. The duration of absence from the terrestrial haul-out site was 2.5 times longer in 1989 than in 1990 (206 vs. 81 h), indicating that walruses used the haul-out more frequently when ice was absent. Direct observations of foraging showed that the walruses were submerged for ca. 81% of the time.

The study documented that (a) natural marks on walruses can be used to study their activity, (b) walruses spend approximately the same amount of time hauling out whether ice is or is not present, (c) they haul out for about 30% of the time, and (d) they are submerged for ca. 80% (4/5) of the time while in foraging areas. This information was used to correct aerial survey counts (Paper 11).

Paper 6 (Topics: **A, D, E**

The status of Atlantic walruses in East Greenland was evaluated on the basis of several historical and recent sources of information on distribution, numbers and catch. Walruses occur in small groups along the coast from ca. 63° N to ca. 81° N. Their greatest abundance is, however, north of ca. 73° 30′ N (i.e. inside the "National Park of North and Northeast Greenland"). The two sexes are segregated during summer. Males generally occupy the inshore foraging areas in Young Sound (ca. 74° 15′ N) and Dove Bay (ca. 76°-77° N) whereas females and subadults summer in the Northeast Water area north of ca. 80° N.

Both sexes winter in this latter area and in smaller polynyas between ca. 70° N and ca. 79° N. Natural marks were used to demonstrate (a) a connection between the groups of walruses using the two inshore feeding areas and (b) long-term fidelity to haul-out sites. Kills by foreign whalers and sealers during the period 1889-1950s severely reduced the population. The present number of walruses in East Greenland is estimated at 500-1000 animals. The true value is likely nearer the high end of that range. Greenlanders removed an estimated 20-30 primarily male walruses (losses included) annually during the 1980s and 1990s, and such a catch rate was probably sustainable.

The study documented that (a) natural marks on walruses can be used to study their gross movements and site tenacity, (b) female walruses occur year-round in the Northeast Water area whereas males occur farther south during summer and (c) the number of walruses in East Greenland remains small. The estimates of abundance and catch were used to model trends in the East Greenland walrus sub-population (Paper 11).

Paper 7 (Topics: **G**)

The reproductive tracts of 152 female Atlantic walruses were analysed. The material was collected between 19 January and 19 November in 1977-78 (n=44) and 1988-1991 (n=108) in Northwest Greenland (eastern parts of the North Water polynya). Females that were classified as being in oestrus (n=23) were taken between 19 January and 25 June. The youngest female that had given birth was 5 years old, indicating that some female Atlantic walruses become sexually mature at 4 years of age. The oldest immature was 8 years, and the oldest animal that had ovulated only once was 11 years. The average age of attainment of sexual maturity (i.e. first ovulation) was 6.1 years (95% CI: 5.2-7.1 years). Fertility rates estimated on the basis of mature females collected during May-November were: 34.6% pregnant, 43.2% postpartum and 22.2% inactive. These proportions did not differ from a model

assuming a 3-year reproductive cycle. Growth in foetal mass and length indicated that implantation occurred on 1 July (95% CI: 26 June-5 July) or 5 July (95% CI: 29 June-11 July), respectively. Newborn calves were observed from January to November. Estimated mean birth date based on observations of 28 newborns was 20 June.

The study documented (a) the age at attainment of sexual maturity and (b) fertility rates, in female Atlantic walruses from Greenland. These estimates were used as input parameters when modeling trends in the Greenlandic walrus sub-populations (Paper 11).

Paper 8 (Topics: **C,F**)

Studies of genetic variation in walruses, using allozymes, mitochondrial DNA (mtDNA) and nuclear DNA (microsatellites), were reviewed. In addition, the genetic relationships of 211 Atlantic walruses from 5 sampling areas west and east of Greenland were studied using 12 nuclear DNA-microsatellite loci and restriction fragment length polymorphisms obtained from the ND1, ND2 and ND3/4 segments of mtDNA. No divergence was observed at the mtDNA level among the 3 sampling areas east of Greenland (i.e. East Greenland, Svalbard and Franz Josef Land), whereas areas west of Greenland (i.e. Northwest and West Greenland) had some differentiation. Genetic variation at the microsatellite loci grouped the individuals into 4 sub-populations: Northwest Greenland (i.e. the North Water), West Greenland, East Greenland and Svalbard-Franz Josef Land. A significant correlation was detected between genetic distance and geographic distance between the sampling areas ("isolation-by-distance effect"), especially at the mtDNA level. A phylogeographic analysis of the mtDNA data indicated that Atlantic walruses have diverged into 2 major groups: one in the North Water and one east of Greenland (i.e. an East Greenland-Svalbard-Franz Josef Land group), whereas the haplotype distribution in the West Greenland sample reflected a mixture of both of those groups. The microsatellite data supported a general grouping of walruses to the west and east of Greenland.

The study (and the other genetic studies of Atlantic walruses that were reviewed) documented (a) the existence of three sub-populations of walruses in Greenland ("West Greenland", "the North Water" and "East Greenland"). This information was used for modeling trends in each of these sub-populations (Paper 11), and for evaluating the effects of climate on walruses in different regions of Greenland ("General introduction, discussion and conclusion").

Paper 9 (Topics: **A,B,F**)

Food consumption of Atlantic walruses was quantified by combining underwater observations of feeding with satellite-telemetry data on movement and diving activity. The study was conducted between 31 July and 7 August 2001 in Young Sound, Northeast Greenland (74° N-20° W). Divers accompanied foraging walruses to the sea floor and collected the shells of newly predated bivalves for determination of number of individual prey and total biomass ingested, per dive. Simultaneously, the activity of a ca. 1200-kg adult male walrus was studied by satellite telemetry during an entire foraging cycle, which included 74 h at sea followed by 23 h resting on land. An average of 53.2 bivalves (SE=5.2; range: 34-89; n=10) was consumed per dive, corresponding to 149.0 g of shell-free dry matter (SE=18.9; range: 62.4-253.1 g), or 2576 kJ (SE=325.2; range: 1072-4377 kJ). During a typical foraging cycle, the estimated daily gross energy intake was 214 kJ per kg body mass (95% CI: 153-275 kJ), corresponding to the ingestion of 57 kg (95% CI: 41-72 kg) wet weight of bivalve biomass per day, or 4.7 (95% CI: 3.3-5.9%) of TBM. Due to ice cover, access to the inshore bivalve banks in the area is restricted to the short summer period, when walruses rely on this ample bivalve resource to replenish their energy stores. It is hypothesised that continued decrease in the extent and duration of Arctic sea ice will increase food availability for walruses in eastern Greenland in the future.

The study used a novel approach by combining underwater observations with satellite telemetry

to document individual food consumption in walruses. The resulting estimate of average daily food ingestion was used to calculate (a) total amount of food ingested by a group of walruses in Young Sound (East Greenland) (Paper 11), and (b) carrying capacity of the walrus foraging areas off West and Northwest Greenland in the "General introduction, discussion and conclusion" section.

Paper 10 (Topics: **G**)

Age at sexual maturity and timing of the mating season were estimated for male Atlantic walruses in the "North Water" sub-population. Testes and epididymides of 174 male walruses (between 0 and 30 yr old) from Northwest Greenland (1987-1990) were examined macroscopically and a subset of specimens from 57 of those animals was analysed microscopically. In physically mature bulls (i.e. ≥12 yr old), sperm or apparently ripe spermatids were found between 9 November and 12 July. In younger walruses, these signs of fertility were found in a few specimens (7 to 11 yr old) collected between 9 January and 28 May. The mating season seems to peak from January-April. The youngest sexually mature individual was 7 yr old and the oldest apparently immature individual was 13 yr old. The sample indicated an average age of sexual maturity of 10.9 yr (95% C.I: 9.6 - 12.2 yr) and that all animals were sexually mature by 14 yr of age. The *non*-spermiogenetic testes and epididymides showed accelerated growth between about the 5-6th and about the 12-15th year of life, indicating that sexual maturation occurs during these years. The length of the baculum increased gradually until about 12-15 yr of age, when physical maturity is attained.

The study determined (a) timing of the mating season and (b) age at attainment of sexual maturity in male Atlantic walruses; this latter parameter had not been estimated previously for Atlantic walruses.

Paper 11 (Topics: **B, F**)

The total consumption of bivalve prey by walruses (*Odobenus rosmarus*) in the impor-

tant 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 4 "walrus seasons". Overall, the animals used ca. 30% of the time in the water inshore in Young Sound between Sandøen and Zackenberg. The remainder of time was used 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 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 (6% of TBM), the corresponding estimate of consumption by walruses is ca. 97 tons SF WW. It is suggested that the two lowest estimates of total consumption are the most plausible.

The study estimated the total consumption rate of selected bivalve species in an inshore feeding area. These data can be used as a "baseline" for studies of trends in the coupling between walruses and the benthic prey populations.

Paper 12 (Topics: **D, E**)

Recent abundance estimates were combined with historical catches and a dynamic age- and sex-structured population model to perform Bayesian assessments of the walrus sub-populations in West Greenland, the North Water, and East Greenland. The model assumed density-regulated dynamics and pre-exploitation populations to have been in population-dynamic equilibrium. It

projected the populations under the influence of the catches to estimate the historical trajectories and assess the current status of the populations. The West Greenland and North Water sub-populations were heavily exploited during the 20th century and current abundance is, at most, only a few percent of historical abundance. Apparently, these populations are still being exploited above sustainable levels. The East Greenland sub-population was heavily exploited after 1889 and during the first half of the 20th century. By 1933, it had been depleted to approximately 50% of its pristine population size. After protective measures were introduced in the 1950s, this population increased to a current level close to its abundance in 1889, and the present rate of removals by hunting appears to be sustainable.

The study (a) established catch series for each of the three sub-populations in Greenland, and (b) involved comprehensive analyses of trends in the sub-populations.

Paper 13 (Topics: A, B, F, G)

An adult Atlantic walrus (*Odobenus rosmarus rosmarus*) male (31 yrs old in 2001) that was tracked by use of satellite telemetry in NE Greenland during four seasons (1989, 1990/91, 2000/01, 2001) revealed a remarkably high perennial tendency of homing and consistency of migration pattern. During all four inshore summering periods (Aug-Sep), the animal used only one terrestrial haul-out from which it made excursions to the same general shallow water area (i.e., likely clam beds) in western Dove Bay (ca. 76° to ca. 77° N). In different years, the size of the inshore foraging area varied between 48 and 86 km^2 in August, and between 136 and 385 km^2 in September. The inshore foraging period lasted ca. 69 days in 1989 and 1990, but ca. 86 days in 2000 (no data for 2001). During fall 1989, 1990/91 and 2000/01, the walrus followed the same migration route in the Greenland Sea north to the wintering grounds in the Northeast Water polynya (ca. 79º to ca. 81º N). Apparently, this movement pattern was relatively independent of annual variations in ice and temperature regimes. Offshore in the Greenland Sea – Fram Strait area, the walrus occurred mainly in areas with dense ice cover (>90%). Both inshore during summer and offshore during winter the animal dived to at least 250 m (maximum depth limit of the transmitter). The tracking of this walrus, whose activity pattern was typical of male walruses in the region, shows that this stenophagous species is a creature of habit with a highly stereotypic movement pattern which apparently is influenced by the location of predictable feeding, wintering and mating areas

The study documented that walruses have a high degree of site tenacity and stereotypic movement pattern. This behavior makes them vulnerable to exploitation and reduces their potential for rapid geographical expansion during times of population growth and favorable climatic conditions, as discussed in the "General introduction, dis-cussion and conclusion" section.

General introduction, discussion and conclusion

1 Part – The effect of hunting

Systematics and taxonomy

Is the walrus a seal or a sea lion?

Scientists have long debated whether pinnipeds are monophyletic or diphyletic. The current view, supported by morphological and molecular data, is that they are monophyletic (e.g. Berta 2002; Deméré et al. 2003). However, there are still conflicting views as to whether the family Odobenidae (walruses) is more closely related to the Phocidae (true seals) or Otariidae (sea lions and fur seals) (Berta 2002). Some studies suggest a sister group relationship between phocids and odobenids to the exclusion of otariids (e.g. Berta & Wyss 1994; Vrana et al. 1994). Other analyses indicate that pinnipeds are monophyletic with odobenids and otariids as sister groups to the exclusion of phocids (e.g Sarich 1969; Lento et al. 1995; Bininda-Emonds & Russel 1996; Arnason et al. 2002). Several life history traits of extant odobenids (i.e. the walrus) and otariids are very similar (see section "Some basic life history traits"), suggesting that the present-day walrus is a type of otariid that became isolated in the Arctic, and that it is in fact the only one that did.

The monophyletic Odobenidae are represented by a single living species, the holarctic *Odobenus rosmarus*, and at least 20 fossil species arranged in 14 genera (Deméré et al. 2003).

Two or more sub-species

The walrus exists as two sub-species that were initially described as separate species (*Odobenus obesus* – Pacific walrus; *Odobenus rosmarus* – Atlantic walrus; Allen 1880). Davies (1958) concurred with Allen (1880) that the two sub-species were worthy of species rank. According to Allen (1880), the two forms differ in facial outline, dimensions of the tusks, certain skull bone characters and body size. Generally, the tusks of the Pacific walrus are larger and thicker and consequently its snout is broader than that of the Atlantic form (Allen 1880; Pedersen 1962; Fay 1982). Furthermore, adult male Pacific walruses have a greater "lumpiness" of the skin on the neck and shoulders than Atlantic males (Allen 1880; Fay 1982).

Based on distribution and morphology, two sub-species are recognized nowadays: Atlantic walrus, *O. r. rosmarus* Linnaeus, 1758, and Pacific walrus, *O. r. divergens* Illiger, 1811 (Fay 1982, 1985). The two sub-species differ genetically (Cronin et al. 1994). However, whether Pacific walruses reach a larger body size is uncertain. Information in **Paper 4**, Wiig & Gjertz (1996) and Garlich-Miller & Stewart (1998) indicates that Atlantic walruses in certain parts of their range may attain the same physical dimensions as Pacific walruses.

Chapskii (1936) proposed that the walruses in the Laptev Sea form a third sub-species (*O. r. laptevi*) that is morphologically intermediate between the Atlantic and the Pacific sub-species. However, that proposal is still disputed (see Fay 1982, 1985). As suggested in **Paper 8**, a genetic comparison of walruses from the Laptev Sea with the other sub-species may resolve this question.

General habitat requirements

The following overview provides a description of the general habitat requirements and some basic life history traits of walruses. My purpose is to emphasize those characteristics that make walruses particularly sensitive to modern exploitation and to point out the limits of their behavioral and ecological plasticity and thus their ability to cope with major ecological changes.

Habitat requirements

Feeding mainly on bottom-dwelling clams (Vibe 1950; Fay 1982), walruses occupy a relatively narrow ecological niche. The distribution of walruses is determined by three basic ecological requirements: (1) Access to areas where the ice is moving and/or not too thick and dense, (2) suitable haul-out sites (either on land or ice), and (3) shallow areas that support mollusks (Harington 1966).

Ice conditions

Walruses can break through solid ice up to ca. 20 cm thick. If the ice becomes thicker than this, they must retreat to areas with lighter ice conditions or moving pack ice (Fay 1982). Therefore, they tend to concentrate during winter in areas where there is moving ice or little ice – and food. Such conditions are found in the major recurrent polynyas (Vibe 1950; Stirling et al. 1981; Fay 1982; Stirling 1997). Atlantic walruses winter in the large polynyas in Foxe Basin in Canada, the North Water in northern Baffin Bay-Smith Sound, the Northeast Water off the northeastern coast of Greenland, and in or near the semi-permanent polynyas off southern Svalbard and around Franz Josef Land (Vibe 1950; Stirling et al. 1981; Fay 1982; Born et al. 1995, 1997; Stirling 1997) – *names of places mentioned in the text can be found in Fig. 2, 3 and 6*. Walruses can also winter in smaller polynyas such as those near Dundas Island and in Hells Gate-Cardigan Strait in the Canadian High Arctic,

and in several places along the eastern coast of Greenland (**Paper 1, 6, 13;** Kiliaan & Stirling 1978; Sjare & Stirling 1996; Born et al. 1997). Individual walruses may show a high degree of perennial fidelity to certain wintering areas (**Paper 13**; Sjare 1993), Photo 1.

Photo 1. Walruses have a remarkable "stereotypy" of movement and great tendency of site tenacity to summering and wintering areas. An adult male was tracked in Northeast Greenland using satellite-telemetry during 4 seasons spanning more than 10 years; 1989-2001 (**Paper 1, 13**). The photo shows the walrus in 1990 when it was 20 years old and was fitted with a ST-3 satellite transmitter and a VHF-radio tag. *Photo: L.Ø. Knutsen.*

Haul-out habitat

During summer, walruses can be found in shallow coastal waters, often in areas with floes of drifting ice that are used for hauling out (Fay 1982; **Paper 5**). According to Fay (1982), mainly females and young prefer such areas, and it is generally assumed that walruses confronted with the choice of ice or land for a resting place always select the ice. However, in several places within their range (e.g. Southampton Island in northern Hudson Bay and Sand Island in Young Sound, East Greenland) Atlantic walruses of both sexes and all age-classes haul out on land irrespective of whether there is ice in the area (**Paper 5**; Salter 1979; Born et al. 1995; Born unpubl. data). Walruses are anatomically and behaviorally adapted to survive in situations where there is no ice during summer (see section "A "warm" challenge to "cool" walruses").

In all parts of their range, Atlantic walruses use terrestrial haul-outs ("*uglit*") during the period from break-up of the land-fast ice in late spring and early summer to formation of fast ice in fall (Born et al. 1995). These haul-outs are usually situated on low, rocky shores or sandy beaches with relatively steep or shelving sub-tidal zones (Loughrey 1959; Mansfield 1959; Salter 1979; Miller & Bonness 1983; Born & Knutsen 1990a). Atlantic walruses exhibit a high degree of fidelity to these haul-outs (**Papers 6, 11, 13**). Born & Acquarone (2001) suggested that several criteria must to be met for walruses to select a site to haul out regularly: (1) The ice must break up at the site early in the season to allow for early access, (2) preferably, the beach or rocky shore must face south to allow for maximum sunlight and warmth when the animals are hauled out, (3) there must be access from more than one side so that it is possible to haul out or return to the water when ice blocks a portion of the beach, (4) the view from the site must allow the walruses to inspect their surroundings, especially the ice situation; (5) it must be possible for arriving walruses to inspect the site from some distance away to determine whether other walruses are there, and (6) foraging areas must be present not too far away (Photo 2). In addition to simple topography, however, it is likely that the group cohesion of walruses is a key factor in determining their "conservative" choice of the same haul-outs year after year.

An important characteristic of walruses is their year-round gregariousness (e.g. Fay & Ray 1968; Fay 1982). This, and their fidelity to predictable near-shore areas (i.e. summering and wintering grounds), makes them vulnerable to modern hunting that involves the use of motorized vessels.

Access to prey

As noted earlier, walruses are highly specialized predators that mainly consume bival-

Photo 2. Several walrus studies have been conducted at the two regularly used terrestrial haul-outs in Greenland – Lille Snenæs in Dove Bay and Sand Island in Young Sound. Both are situated in the "National Park of North and Northeast Greenland". The photo shows Lille Snenæs where studies were conducted between 1989-2001 (Acquarone 2004; **Paper 1, 2, 5, 6, 13**). The photo was taken in August 1990 when ice floes were absent in Dove Bay and the walruses therefore only hauled out on land.
Photo: E.W. Born.

ves (Vibe 1950; Fay 1982*)*. They feed on a variety of bottom-dwelling invertebrates, including 9 phyla (Fay 1982). However, only a few bivalves – usually *Mya* sp., *Hiatella* sp. and *Serripes* sp. – make up the bulk of their diet (Vibe 1950; Fay 1982; Fay et al. 1984a; Gjertz & Wiig 1992; Fisher & Stewart 1997; Sheffield et al. 2001; **Paper 9**). Also, several species of seals, for example ringed seals (*Phoca hispida*), are taken and could play a significant role in the diet (Mansfield 1958; Fay 1982, Smith et al. 1979; Lowry & Fay 1984; Fay et al. 1990; Timoshenko & Popov 1990). Seals made up to 3-11% of the food in the Bering Strait – Chukchi Sea region (Lowry & Fay 1984). It is certain that seals are actively killed and consumed rather than being eaten only as carrion (Fay et al. 1990). In addition, various fishes (sand lance, *Ammodytes* sp., and polar cod, *Boreogadus saida*; Fay & Stoker 1982; **Paper 3, 6**) and sea birds are taken (Fay et al. 1990; Gjertz 1990; Mallory et al. 2004). Fay (1982) suggested that walruses select bivalves preferentially and that other food is consumed opportunistically. There are, however, indications that as walruses approach

the carrying capacity of bivalves in a given area, they may shift their diet towards other benthic invertebrates as well as certain vertebrates (Fay & Stoker 1982). It is suggested that walruses in Northeast Greenland survive the winter offshore at deep waters by feeding facultatively on seals and fish (**Paper 6**).

Satellite-telemetry and studies of dive activity involving satellite-linked dive-recorders (SDR) and time-depth-recorders (TDR) have revealed that walruses forage mainly at depths <40-50 m during summer (Wiig et al. 1993; Jay et al. 2001; Gjertz et al. 2001; Acquarone et al. 2004a; **Paper 11**). However, dives to ca. 180 m have been recorded for Atlantic walruses inshore in Canada (Stewart 2001) and to at least twice as deep at Svalbard (C. Lydersen, pers. comm. 2004). In Greenland and the Canadian High Arctic, walruses move inshore after break-up of the land-fast ice to exploit the shallow-water mollusk banks during the relatively brief open-water season (Born et al. 1995; **Paper 6**). In Northeast Greenland, dives have been recorded to 250+ m both inshore and offshore (**Paper 13**).

Some basic life history traits

Walruses are the largest pinnipeds in the Arctic (King 1964). They are relatively long lived, grow slowly, have delayed onset on sexual maturity, and produce few offspring per cycle but invest heavily in each calf or pup (King 1964; Fay 1982). These are typical life history traits of large animals (Bonness et al. 2002). All other Arctic seals are phocids with smaller body size and a greater reproductive capacity (Ibid.).

Otariids are generally small in body size compared with most phocids (Costa 1993). The walrus is the only "otariid-like" pin-niped that has come to inhabit Arctic waters, and its large body mass is likely a significant factor in its successful adaptation to Arctic conditions. Large body size is energetically an advantage in cool environments, and Arc-tic (and Antarctic) phocids, except ringed and harbor seals (*Phoca vitulina*), have comparatively large total body mass, TBM

Table 1. Total body mass (TBM), growth rate, duration of lactation period and estimates of "harem" size in free-ranging Atlantic and Pacific walruses.

Sub-species	Location	Birth TBM[1] ♀♂ kg	Weaning TBM ♀♂ kg	Growth rate ♀♂ kg/day	Adult TBM[2] ♀ kg	♂ kg	Nursing duration days	"Harem" size no. ♀
O.r.rosmarus	NW Greenland	60[3]	220-270[4]	0.3	720	1114	548-730[5]	12-13[6]
	Hudson Bay				550	1237		
	Foxe Basin[7]	57[3]			635	858		
O.r. divergens	Bering Strait	63	ca. 250		861[8]	1278[8]		10[9]
	Bering Strait				702	1305		

1: TBM=Total Body Mass.

2: Assymptotic TBM (data from **Paper 4** except Foxe Basin).

3: Based on predicted standard body length at birth (**Paper 7**) and **Paper 4** (table II, eq. 1).

4: TBM based on **Paper 4**, eq. 7a,7b (weaning at 1.5 and 2.0 years of age, respectively).

5: Weaned between 1.5 to 2 years of age (Fay 1982).

6: This study, see text.

7: Source: Garlich-Miller & Stewart (1998).

8: TBM calculated from data in Fay (1982) who, however, mentioned (p. 34) that assymptotic TBM in females and males are roughly 830 kg and 1200 kg, respectively.

9: Fay et al. (1984b).

(Ibid.). In comparison with other Arctic seals, which forage most of the time in a three-dimensional space, walruses generally forage on prey that are restricted to a two-dimensional habitat in shallow waters. Resources restricted to two dimensions are generally much easier to monopolize and defend than resources in a three-dimensional space. Thus, given that larger individuals are superior over smaller individuals in interference competition, one may expect a stronger positive co-variance between body size and the resources available in the localized habitat of walrus populations in comparison to other populations of seals (Witting 1997, 2003).

Similar to other polygynous marine mammals, male walruses are larger than females. On average, the TBM of adult male walruses is 1.4-2.2 times that of adult females (Table 1). Furthermore, male walruses do not attain social maturity until 5-7 years after attainment of physiological sexual maturity (Fay 1982), by which time they have reached a TBM that allows them to compete successfully for females. The "secondary growth spurt" associated with

attainment of social maturity in male Pacific walruses (Fay 1982, fig. 19) has not been observed in Atlantic walruses (**Paper 4**; Mansfield 1958; Garlich-Miller & Stewart 1998). However, it may be worth noting that the growth equation in **Paper 9**, which included a ca. 31 year old, 1629 kg male, indicated that the TBM of male Atlantic walruses may continue to increase long after sexual maturity has been reached and that most males may never reach their full physical growth potential (Fig. 1).

Generally, the life history traits and vital parameters of walruses resemble those of otariids more than those of phocids. It may be hypothesized that walruses are the only otariid-like pinnipeds that managed to occupy the Arctic and that many of their life history traits and their adaptation to life in the Arctic reflect their evolution at lower latitudes. This hypothesis is supported by a comparison with the adaptations of modern otariids. The otariids representing the earliest lineage to survive to modern times evolved ca. 11 Ma B.P. (i.e. million years before present) (Berta & Adams 2000) in temperate waters of the North Pacific (Gentry 2002). They now occupy cool sub-polar, temperate and tropical regions with breeding sites between 55º N and 60º S. Otariids are absent from the North Atlantic region but widespread and diverse in the North Pacific and Southern Ocean (Gentry 2002; Martin & Reeves 2002).

Walruses and otariids differ fundamentally from phocids in parental care and mating systems. Prior to parturition, female phocids have accumulated body lipid reserves (blubber) that supply their own metabolic needs and the demands from milk production during what is usually a brief lactation period (Kovacs & Lavigne 1992). In contrast, otariids alternate between feeding at sea and nursing on shore during the lactation period that lasts for 4 to 12 months, depending on the species (Ibid.). Walruses feed their young
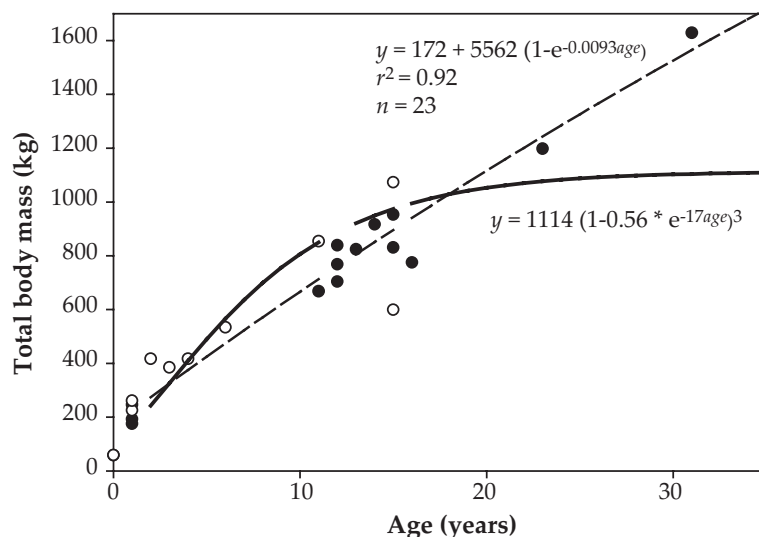
Fig. 1. Total body mass (TBM) of male Atlantic walruses from Greenland (black circles, n=13) and Canada (open circles, n=10; extracted from Mansfield 1958: fig. 13). The von Bertalanffy growth curve in **Paper 4** (fig. 2, equation 7b) (solid line) and the growth curve fitted to the data points (hatched line) are shown. TBM of three 0-1 year old females (**Paper 4**) from Northwest Greenland were included to improve the predictive power of the new equation.

In the figure:
$$y = 172 + 5562 (1-e^{-0.0093age})$$
$$r^2 = 0.92$$
$$n = 23$$

$$y = 1114 (1-0.56 * e^{-17age})^3$$

for 18-24 months, sometimes longer, but after ca. 5-6 months some calves begin to feed on benthic animals as well. The mother feeds during lactation and the calves accompany their mother during feeding (Fay 1982).

The larger body fat reserves relative to body mass in female phocids allow for an uninterrupted, energetically efficient nursing period, and weaning can be achieved in a short period of time. Otariids and walruses have proportionally less ample blubber stores prior to parturition, and they forage during nursing (Bonness & Bowen 1996). Blubber constitutes ca. 18-26% of TBM in otariids and walruses (**Paper 4**; Bonness & Bowen 1996; Acquarone & Born 2004) and 25-42% in phocids (Bonness & Bowen 1996). The agility required for their swimming style and mode of locomotion on land (or ice in case of walruses) may limit how much fat they can store.

Pinnipeds require ice or land for giving birth and nursing the pup (Bonness & Bowen 1996). Walruses usually give birth on ice and occasionally in the water (Fay 1982: 202) but in contrast to other pinnipeds they can also nurse when in the water (Miller & Bonness 1983; Fay 1982). This "aquatic nursing strategy" of walruses implies that the calf remains with its mother wherever she goes. In contrast, otariids (and some phocids like the relatively small ringed and harbour seals) use a "foraging cycle" strategy in which the female leaves the pup on a terrestrial haul-out (or ice in case of the ringed seal) and makes foraging excursions during the relatively long lactation period. However, many phocids use the "fasting strategy" where the females arrive at the breeding site with large blubber stores. These energy stores are used for lactation and for the females' own energy requirements during the short nursing period (Bonness & Bowen 1996).

Otariids and walruses grow more slowly and are fed for a longer period than are phocids (Kovacs & Lavigne 1992; Bonness & Bowen 1996). Growth rate in Atlantic walrus calves is "otariid-like", but a little slower than in otariids (ca. 0.3 kg/day; Table 1). The estimate of growth rate in Table 1 is somewhat lower than that given by Kovacs & Lavigne (1992: 0.4 kg/day). The discrepancy is caused by a higher estimated weaning age (hence body mass) by those researchers than by me.

A prolonged lactation period is an advantage when rearing the calf in an environment where ice conditions vary. For instance, in years when ice conditions are severe and the fast ice covering inshore feeding banks does not break up, or breaks up late, thereby limiting the access of walruses to good feeding sites, the effect on the calf may be ameliorated because it can continue to obtain milk from its mother. Furthermore, a prolonged lactation period gives the young animal more time to develop swimming and foraging skills (Kovacs & Lavigne 1992). It is also likely important that walrus calves learn where the mollusk banks are located, and that they learn this over an entire annual cycle in which the summer and winter feeding grounds are in different places (e.g. West Greenland and North Water walruses).

When weaned at 1.5-2 years of age, the Atlantic walrus calf weighs ca. 220-270 kg (**Paper 4**), which means a relatively high "calf TBM/mother TBM" ratio compared to that of other pinnipeds (Kovacs & Lavigne 1992). This relatively large mass at weaning is likely an advantage in the specialized feeding of walruses. The calf must be able to dive to the seafloor and forage there for several minutes at a time (Fay 1982).

The potential for males to fertilize mates is highest when receptive females are moderately asynchronous and spatially clumped (Emlen & Oring 1977; Bonness 1991). The breeding season of walruses tends to be less synchronous than that of most phocids and otariids (Bonness et al. 2002). Walruses have an extended breeding season. Female Atlantic walruses are in estrus from mid January to late June (**Paper 7**), and the males can be fertile from early November until mid July (**Paper 10**). In Pacific walruses, estrus in some females may occur as early as December and as late as August. Most old bulls are potent from November-March and the younger bulls from December/January-May (Fay 1982). Apparently, the peak of the mating season in walruses is January-April (**Paper 7**; Fay 1982; Fay et al. 1984b; Sjare & Stirling

1996) but there might be some regional variation. The extended breeding period of walruses may reflect an adaptation to variable ice conditions (as opposed to predictable access to a rookery or terrestrial haul-out), and the fact that walruses do not depend on a substrate of land or ice for mating or giving birth.

During the mating season, adult male walruses engage in a ritualized visual and acoustical display in the water (Fay et al. 1984b; Sjare & Stirling 1996; Sjare et al. 2003). Sjare & Stirling (1996) described the breeding system of Atlantic walruses in the Canadian High Arctic as "female-defence polygyny," where individual mature males monopolize access to herds with potentially reproductive females for extended periods of time. The mating system of Pacific walruses has been described as being more like a "lek" system in which potent males defend small display territories near a herd of mature females (Fay et al. 1984b). The extended breeding season, a relatively loose group structure (except for the female component from February-early April; Sjare & Stirling 1996), the widespread distribution of females (and other walruses) in the wintering habitat (Ibid.), and the fact that mating occurs in water (Sjare & Stirling 1996) make it impossible for male walruses to monopolize many females simultaneously as is the case in phocids and otariids that either mate in dense patches on the ice (e.g. hooded seals, *Cystophora cristata*, and harp seals, *Pagophilus groenlandicus*) or on rookeries (otariids).

In the study by Sjare & Stirling (1996), male Atlantic walruses had access to 1-5 adult female herd members although this range does not necessarily represent an estimate of "harem" size. The ratio of adult male Pacific walruses to adult females was estimated as 1:10 on the breeding grounds (Fay et al. 1984b). According to Kovacs & Lavigne (1992), who cited various sources, Atlantic walrus "harem" size is 5.0 whereas the average "harem" size in the Pacific walrus is 9.4. There is a significant direct relationship between "harem" size and male TBM in phocids and otariids (Lindenfors et al. 2002). In 35 extant species and sub-species of phocids and otariids, "harem" size is correlated with $\log_{10}$ TBM (Ibid.) (Log "Harem size", i.e. number of females=-1.243 + 0.771 * log TBM (kg) (P=0.001; F=13.02; df= 1/34; r^2 = 0.277; based on data from the appendix in Lindenfors et al., 2002, but *not* including data of the two walrus sub-species). According to this relationship, the predicted average "harem" size of Atlantic walruses in Greenland (asymptotic body mass of males=1114; **Paper 4**) would be 12-13 females (Table 1).

A factor that makes walruses vulnerable to exploitation is their relatively low reproductive capacity compared with other Arctic seals. Average age at attainment of sexual maturity (first ovulation) in female Atlantic walruses in Greenland is ca. 6 years. The reproductive cycle is basically triennial meaning that adult females give birth every third year (**Paper 7**) usually to a single calf (Fay 1982). Atlantic male walruses become sexually mature between 7 and 13 years of age (average age: 11 years) (**Paper 10**). However, Pacific walruses usually do not participate in the mating until they are physically mature at 13-16 years (1982) and the same is probably the case in Atlantic walruses.

Assuming an even sex ratio, maximum sustainable yield rate for the mature component of the population was estimated at 2% (95% CI: 0-7%) for the West Greenland and Northwater sub-populations and 4% (CI: 0-10%) for the East Greenland population (**Paper 12**). Estimates of annual net increase in other studies of walruses range between 1 and 8% (cf. "Discussion" in **Paper 12**). For comparison, an annual breeder like the ringed seal may have an annual population crude production about 20% (Miller et al. 1982) and a net population increment of ca. 11% per year (Smith 1973).

Homing behavior and site fidelity

Several species of marine mammals show a clear tendency to home – i.e. to return regularly to the same area (cf. Papi 1992). Homing behavior is strongly developed in walruses. Their great homing tendency and site fidelity are likely fundamental to the establishment of walrus sub-populations. These characteristics also may help explain

the rate and extent to which walruses have been able to expand their geographical distribution.

Photo-identification of walruses at the Lille Snenæs haul-out in Dove Bay (ca. 77° N), Northeast Greenland, demonstrated a great tendency of some individuals to return to this site each summer. The identification of two individuals in 1990 that had been photographed there in 1982 and 1986, respectively, demonstrated long-term site fidelity (**Paper 6**). Similarly, the walruses at Sand Island in Young Sound (Photo 3) show a tendency to return to this haul-out each summer, as revealed by photo identification and genetic marking in 2002 and 2003. At that site the same adult male was tagged there during August 1999, 2000 and 2001 (Table 2: footnote 8) and he was subsequently re-identified visually on the haul-out each summer through 2004 (Born unpubl. data). Furthermore, of a total of 38 genetically identified individual walruses that used the Sand Island haul-out in 2002, 45% were re-identified genetically at the haul-out in 2003 (Born & Andersen, unpubl. data).

The remarkable "stereotypy" of movement and great tendency of site tenacity was seen in an adult male (Table 2) that was tracked using satellite-telemetry during 4 seasons spanning more than 10 years. Each season the animal used the same haul-out and summer feeding area. During two winters, when it was possible to track him, he also used the same wintering ground (**Paper 13**).

Despite this site tenacity, walruses have expanded their range during post-glacial times (Dyke et al. 1999) and in areas such as Svalbard and East Greenland they are in the process of expanding their range after depletion by hunting (Born 1984; Gjertz & Wiig 1994; Born et al. 1995; **Paper 6**). As walruses expand their range, it is likely males, and perhaps in particular subadult males, that explore new areas. In several

large mammal species, there is a greater tendency for subadults, especially males, to disperse (e.g. Greenwood 1980; Shrader & Owen-Smith 2002; Ferreras et al. 2004). Most of the walrus stragglers that have visited the coasts of Europe and North America were presumably males (Ritchie 1921; Bruun et al. 1968; Mercer 1976; Gjertz et al. 1993) and among stragglers observed along the coasts of Norway since 1967 there seems to have been a surplus of subadult males (Gjertz et al. 1993).

Photo 3. The Sand Island in Young Sound (Northeast Greenland) in August 1999. Each summer a group of about 60 walruses use the about 600 x 800 m island for resting in between foraging excursions (**Paper 11**). The entrance to Young Sound is to the right=east. *Photo: E.W. Born.*

A philosophical interlude- or "summary": The generally sedentary nature of walruses during winter and the inherent gregariousness of females appear to have been important factors influencing the evolution of the species' social behavior and mating system (Sjare & Stirling 1996). Likely, these factors also have been driving forces behind the establishment of genetically different sub-populations of Atlantic walruses (see section "Identification of sub-populations of walruses").

The early walrus-types that lived at lower latitudes under more favorable weather conditions with no ice (cf. **Appendix I**) probably used terrestrial roo-

keries during the breeding season, similar to the extant otariids. During the mating season the tusks could be used for ritual displays and to defend "harems" on land. However, when they changed to mating during the Arctic winter (and it is unclear when this happened) walruses inevitably had to retreat to the water where temperatures are much more favorable than on land. During this shift from land to water in areas where the ice cover is variable, and to a large extent also unpredictable, they became independent of highly localized breeding sites (rookeries). The relatively asynchronous mating period in walruses may reflect an adaptation to a highly variable environment that does not allow all members of the group to meet in a highly concentrated area during a brief period of time. Acoustical displays underwater (instead of visual displays on land) appear to be the solution for a polygynous species that does not use terrestrial mating grounds.

Walruses depend on being able to remember where clam banks are located and therefore show a high degree of fidelity to such foraging sites. This likely limits the incentive for an individual to explore new areas. The relatively slow expansion of walruses into new or previously occupied areas may reflect the fact that members of a population need to discover new foraging habitat essentially by chance. Awareness of a new feeding ground must then spread among group members before the habitat becomes a regularly used resource. This was likely the mechanism behind the gradual re-colonization of the North Atlantic Arctic after the last ice age (**Appendix I**) and the more recent return of walruses to Svalbard through immigration from Franz Josef Land (Born 1984; Gjertz & Wiig 1994).

Their high degree of site tenacity in combination with an inability to expand their range quickly and low reproductive capacity make walruses highly vulnerable to exploitation.

Present distribution, abundance and the effect of hunting

Walruses presently have a disjunct Holarctic distribution in which the widest gap of ca. 500 km is between the eastern Chukchi Sea and the western Canadian High Artic (Fay 1985) (Fig. 2).

The distribution of Atlantic walruses and population sub-structure

Atlantic walruses are distributed from the Canadian Arctic to the western Russian Arctic (Fig. 3). The western limit of regular occurrence is in the vicinity of Bathurst Island (ca. 100º W) (Born et al. 1995) but there are extralimital records to the west of this area (Harington 1966). The eastern limit of Atlantic walruses is not well established. Walruses occur at Severnaya Zemlya (90-105º E), and in the Laptev Sea they are found principally in the western parts along the eastern Taimyr coast (ca. 115° E) and near the Lena Delta. Apparently, the ranges of Atlantic and Laptev walruses meet in the Severnaya Zemlya-eastern Taimyr area (Born et al. 1995). However, present information is insufficient to determine to which demographic unit (or sub-species) the walruses in this region belong.

A biological population consists of the individuals that belong to a single reproductive pool. They form a self-contained unit, with emigration and immigration rates far lower than the intrinsic rate of population growth (Anon. 2002a). A sub-population may be defined as one of several geographically or otherwise distinct groups within a larger population among which there is little exchange (Molloy et al. 2002). This definition of a "sub-population" is adopted here.

Based on information on current distribution, migration patterns and catch history, Born et al. (1995) suggested the existence of at least eight sub-populations of Atlantic walruses (Fig. 3). Three of these putative sub-populations occur at least partly in Greenland: the West Greenland, North Water (Baffin Bay-eastern Canadian High Arctic) and East Greenland sub-

populations (i.e. 4, 5 and 6 in Fig. 3).

West Greenland is defined here as the area between Kap Farvel (the southern tip of Greenland) and 76° N (i.e. the northern limit of the Melville Bay and the ap-

proximate southeastern limit of the North Water polynya, Fig. 6).

Northwest Greenland is defined as the area from 76° N to 80° N in Kane Basin, thus including the central part of the Qaanaaq

Fig. 2. The approximate distribution of Atlantic, Pacific and Laptev walruses. Modified from Fay (1985).

Fig. 3. Map showing the approximate distribution of the proposed Atlantic walrus sub-populations (Born et al. 1995). Samples included in the genetic studies by Andersen et al. (1998), Andersen & Born (2000) and **Paper 8** came from areas inhabited by the putative stocks number 4, 5, 6 and 7. The study by Andersen et al. (2004) also included samples from the putative stocks 2 and 3.

municipality of Northwest Greenland. Walruses in this area belong to the "North Water" sub-population that also ranges into the eastern Canadian High Arctic (Fig. 3).

East Greenland encompasses the eastern coast of Greenland between Kap Farvel and ca. 82° N (Nordostrundingen).

Physical and ecological conditions in the "walrus areas" in Greenland

In Greenland walruses occur in three main distribution areas (Central West, Northwest and East Greenland) that differ with respect to their physical and biological conditions. As background for understanding the historical and present status of walruses, I summarize the important features of the physical and ecological environments of those areas in Greenland where walruses occur.

Walruses are generally confined to areas with shallow water (Fay 1982). The continental shelf of Greenland attains a maximum width of ca. 300 km in Northeast Greenland but narrows to ca. 35 km in the south (Fig. 4). This shelf is predominantly one of sediment accumulation (Funder & Larsen 1989).

West Greenland
Oceanography and ice conditions: In West Greenland, areas with <100 m depth are found in a narrow strip along the coast north to 76° N, except in the central areas between ca. 66° N and ca. 68° 15' N, and along the western side of Qeqertarsuaq/Disko Island (Fig. 4). Extensive banks in these areas are the main wintering quarters of walruses in West Greenland (**Paper 3**).

West Greenland is influenced by the inflow of the relatively warm north-flowing West Greenland Current (a branch of the Irminger Current) that has mixed with polar water from the East Greenland Current (Riget et al. 2000), Fig. 5. The West Greenland Current reaches as far as north 77°-78° N in the eastern parts of the North Water polynya in Northwest Greenland (Melling et al. 2001). The present overall current pattern was probably established 9-8 Ka B.P. (kilo/1000-years before present) (Dyke et al. 1996) - i.e. not long after the last de-glaciation of Greenland.

Upwelling and mixing of water masses of different origin at the Central West Greenland banks (Buch 2001) make these areas highly productive, and during the 20th century they were main areas for large fisheries for halibut (*Hippoglossus hippoglossus*)
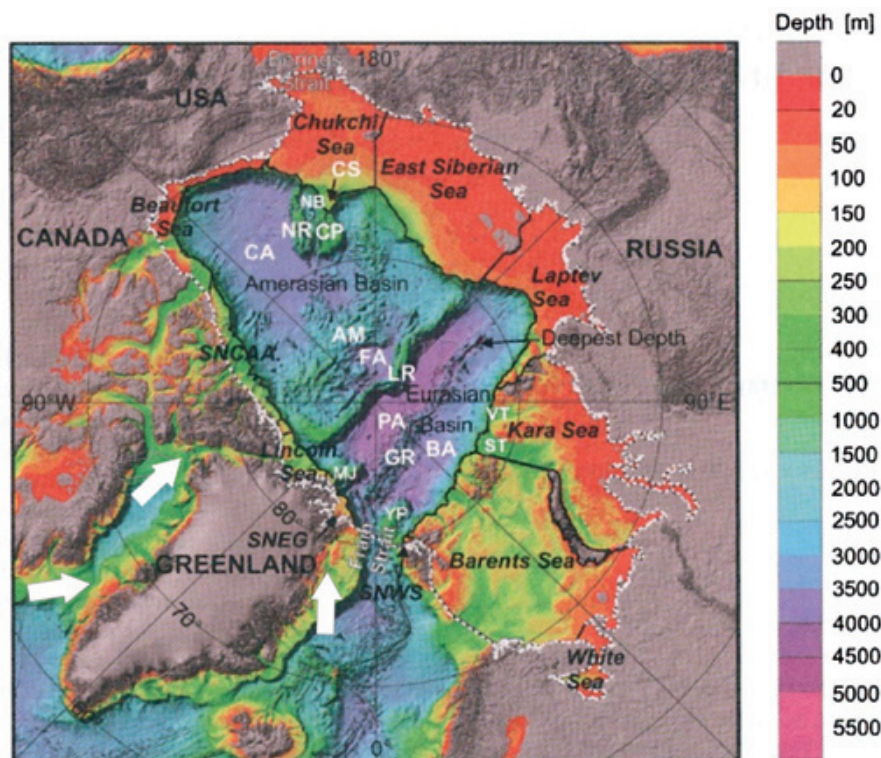

Fig. 4. Map of the bathymetry in the Arctic oceans. Source: Stein & McDonald (2004). The three areas where walruses winter in Greenland are indicated with arrows.

and Atlantic cod (*Gadus morhua*) (Hansen 1949; Smidt 1983; Hamilton et al. 2003).

Due the influx of warm Atlantic waters the coastal areas south of ca. 68° N usually have little ice or are free of ice during winter. With some annual variation in geographical position, the edge of the northeastern Davis Strait-southeastern Baffin Bay pack ice (the "West Ice") is situated relatively close to the coast between ca. 65° N and ca. 68° 45' N (McLaren & Davis 1981) where it is usually present between October and May (Vibe 1967; Buch 2001). Hence, the walrus grounds in the Sisimiut-Aassiaat area and along Qeqertarsuaq/Disko Island are usually devoid of ice between May-June and November-December.

Benthic food: Molluskan records in West Greenland date back to ca. 10 Ka B.P. (Dyke et al. 1996; Bennike & Björck 2002). Important walrus food items like *Mya*, *Hiatella*, *Macoma* and *Serripes* have been recorded and dated to 9-7 Ka B.P. in the historically important walrus areas at the entrances of the fjords Nassuttooq/Nordre Isortoq and Nordre Strømfjord (Kelly 1973), Fig. 6. During 8-5 Ka B.P. diversity of mollusks increased due mainly to immigration of boreal elements (Funder & Weidick 1991; Dyke et al. 1996).

West Greenland is characterized by bivalves of sub-Arctic waters. The boundary between Arctic and sub-Arctic waters in this region, as determined by the distribution of certain boreal littoral animals, is at ca. 73° N (Madsen 1936, 1940). The sub-Arctic region in Davis Strait-Baffin of bivalve fauna also includes southeastern Baffin Island and the eastern coast of Labrador (Lubinski 1980).

Fig. 5. Map of the major currents and ice cover in the Arctic oceans. In Greenland major polynyas are found in northern Baffin Bay (the North Water) and in Northeast Greenland (the Northeast Water) and at the entrance to Scoresby Sound in East Greenland. Source: Slightly modified from Stein & McDonald (2004).

Walrus food items such as *M. truncata, S. groenlandicus, H. arctica, M. baltica* and *Astarte borealis* (*calcarea*) are distributed in shallow waters in West Greenland (e.g. Vibe 1939; Marin ID 1978; Petersen 1978; Lubinski 1980; Schmid & Piepenburg 1993). Walruses have been reported to feed on *S. groenlandicus* and *Mya* in the Sisimiut-Aasiaat area (**Paper 3**).

Northwest Greenland (the North Water)

Oceanography and ice conditions: The environmental conditions in Northwest Greenland are influenced by the North Water polynya in northern Baffin Bay and Smith Sound (Fig. 6). The North Water is one of the largest recurrent polynyas (70000-80000 km^2) in the Arctic (e.g. Born et al. 2004 and references therein). During winter ice coverage is less dense in the polynya than in the surrounding areas (Smith & Rigby 1981).

Banks with <100 m water depths are found along the coasts of the North Water, and extensive shallow-water banks with <100 m depth are found particularly on the eastern side of the polynya (Vibe 1950; Born et al. 2004), Fig. 4.

An extension of the relative warm West Greenland Current reaches the eastern parts of the North Water whereas a current of polar water flows south along its western parts (i.e. along eastern Ellesmere Island) (Kiilerich 1933; Grøntved & Seidenfaden 1938; Melling et al. 2001). This current pattern, in combination with primarily northerly winds, keeps the polynya open during winter – and generally it is warmer and ice conditions are less severe in its eastern than in its western parts (e.g. Barber et al. 2001). As a consequence, animal life is generally richer on the eastern side of the polynya, and walruses can forage there during winter (Vibe 1950).

The North Water begins to open by May and during August-September the eastern areas (i.e. the Qaanaaq municipality) are usually devoid of ice. By late October the edges of the polynya have formed again (Smith & Rigby 1981). Smaller persistent open (or semi-open) water areas where walruses from the North Water population can winter are also found at the entrance to

Jones Sound off Coburg Island, in Hells Gate-Cardigan Strait in western Jones Sound and in Lancaster Sound off the southeastern coast of Devon Island. Such areas with relatively light ice conditions during winter exist in Greenland around Northumberland Island, and between Saunders Island and Wolstenholme Island (Vibe 1950; Smith & Rigby 1981; Born et al. 1995 and references therein). Walruses may also winter in small leads and cracks in the dense ice adjacent to the North Water in the Canadian High Arctic archipelago (Sjare & Stirling 1996; Sjare et al. 2003; Born unpubl. data) or/and in the shear zone between the Baffin Bay pack ice and the fast ice along the northern parts of West Greenland (Born et al. 1995), Fig. 6.

Benthic food: The molluskan fauna of Northwest Greenland and adjacent Canadian areas is high-Arctic (Lubinski 1980; Dyke et al. 1996). The oldest bivalve (*H. arctica*) from this region, dated to nearly 15 Ka B.P., indicates that at least that species survived the Last Glacial Maximum, LGM, there (Dyke et al. 1996). Only four species (also including *Mya*) are recorded from these areas before 10 Ka B.P. However, the diversity of bivalves increased during 10-8 Ka B.P., with the dominant additions to the bivalve fauna being *Astarte* sp. and *M. calcarea* (Ibid.).

Few bivalves are present around Savissivik (ca. 76º N) at the southeastern edge of the North Water (Vibe 1939), so there is little possibility for walruses to forage in that area (Vibe 1950). However, the shallow-water banks of the North Water area are rich in bivalves and other benthos suitable as walrus food (Vibe 1950). In the Appat/Saunders Island (ca. 76° 30' N) and Murchinson Sound (ca. 78° N) areas the *Macoma* community, with a variety of typical walrus prey, is widely distributed in shallow waters. *Macoma, Hiatella, Astarte* and *Serripes (Cardium)* were the most important bivalves by weight in bottom samples from the bank, and stomach analyses showed that *Mya* was also important as walrus food (Ibid.). Dredging in 2002 showed the presence of *Mya, Serripes* and *Chlamys islandica* at Saunders Island and in the eastern part of Murchinson Sound (Glahder et al. 2003).

Important walrus prey (e.g. *Nucula,*

Astarte, *Serripes*, *Yoldia*, *Portlandia*, *Macoma*, *Mya* and *Hiatella*) is also found on the western side of the North Water and in waters of the Canadian High Arctic archipelago (Lubinski 1980).

East Greenland

Oceanography and ice conditions: In East Greenland walruses are mainly distributed north of Scoresby Sound (71° 30ʹ N)(**Paper 6**) and the description of the marine environment therefore focuses on the conditions in Northeast Greenland.

The bathymetry of East Greenland is not well charted. Areas with <100 m water depth are generally restricted to a narrow strip along the coast south of the entrance to Scoresby Sound. However, farther north, banks are found between the Hold-with-Hope/Gael Hamkes Bay area (ca. 73° 30ʹ N) and Shannon Island (ca. 75° N), in the Dove Bay area (76°-77° N), and particularly between ca. 78° N and Nordostrundingen where the Northeast Water polynya is located (Schneider & Budéus 1997).

The marine environment is strongly influenced by the East Greenland Current that brings cold polar water and multi-year pack ice southward along the coast all year round (Aagaard & Coachmann 1968; Martin & Wadhams 1999), Fig. 5. In the areas inhabited by walruses the solid land-fast ice covers the fjords for 7-8 months in the southern areas and 9-10 months in the north (Rysgaard et al. 2003a). Fields of multi-year pack ice, originating mainly from the Polar Ocean, are found along much of the coast even during summer (Holm & Petersen 1921; Martin & Wadhams 1999), Fig. 5.

Polynyas where walruses winter are located at: Northern Blosseville Coast, the entrance to Scoresby Sound, the Gael Hamke Bay-Shannon Island area, east of Store Koldewey, Île de France (renamed in 2004 to Qeqertaq Prins Henrik), and the Nordostrundingen (**Paper 6**).

Benthic food: Knowledge of the bivalve fauna is comparatively great on the sparsely inhabited east coast of Greenland. The East Greenland bivalve fauna was dominated by a restricted Arctic assemblage from de-glaciation until 6.5 Ka B.P., with *Mya* and *Hia-tella* exceedingly abundant. More thermophilic bivalve species occurred from ca. 8 to ca. 4 Ka B.P. (Dyke et al. 1996).

Bivalves including *Serripes, Mya* and *Hiatella* have been found along the coast of East Greenland from the Ammassalik area north to Dove Bay. Densities are relatively high and, at least locally, walrus food is abundant (Thorson 1933, 1934a,b, 1937; Berthelsen 1937; Ockelmann 1958; Piepenburg & Schmid 1996; Schiøtte 1989; Sejr et al. 2000, 2002; Sejr 2005). However, in many of the fjords water depths >100 m are within ca. 100 m of the shore, which limits potential walrus feeding areas to a narrow coastal zone (Berthelsen 1937). Generally, densities of bottom-dwelling invertebrates are higher along the outer coasts than in the inner parts of the fjords (Thorson 1937). Extensive banks (i.e. Ob, Belgica and AWI banks) with <150 m depths are found in the Northeast Water area (Schneider & Budeus 1997; Piepenburg et al. 1997). Walruses winter there (**Paper 6, 13**), testifying to the existence of benthic prey in this polynya. In the Northeast Water *H. arctica, M. calcarea*, *M. truncata*, *Portlandia arctica* and the gastropod *Margarites groenlandicus* are present near shore. The latter two species, which are known walrus food items (Fay 1982), were found in relatively high numbers (Weslawski et al. 1997). However, the benthic megafauna in the Northeast Water is dominated by brittle stars, sea urchins and various amphipods and shrimps (Piepen-burg 1988; Piepenburg & Schmid 1996; Weslawski et al. 1997). Farther north, *Astarte, Macoma*, *Mya* and *Hiatella* were among bivalves recorded in Jørgen Brønland Fjord (ca. 82° 10ʹ N - 30° W, i.e. north of Nordost-rundingen), with the highest densities found in <20 m depths (Schiøtte 1989). However, walruses have not been documented in that area in historical times (**Paper 6**).

In summary, in eastern Greenland food for walruses appears to be abundant, at least locally, but suitable walrus habitat is limited to a few areas with shallow water and relatively light ice conditions during winter.

Fig. 6. Approximate distribution during winter of the three sub-populations of walruses in Greenland. Walruses from the West Greenland and North Water sub-populations summer in Canada. It has not been determined to which sub-population walruses between Nussuaq and Savissivik belong. The approximate position of the edge of the pack ice at its maximum extension and the location of polynyas are indicated.

Distribution of walruses in Greenland

Walruses are found on the eastern and the western coasts of Greenland (Figs. 3,6). At the local scale, their distribution has changed during the last ca. 100 years primarily due to hunting (see section "Change in distribution").

Identification of sub-populations of walruses

Identification of population structure and sub-structure is a key aspect of wildlife management (Anon. 2002a). It is also crucial for evaluating how hunting and environmental change have affected – and may affect – walruses in different parts of Greenland. Socio-economic changes, hunting strategies and environmental regimes differ markedly among the three regions of Greenland inhabited by walruses.

Several studies have elucidated the population structure and sub-structure of walruses in Greenland.

Genetic analyses: A study aimed primarily at exploring differences in mitochon-

drial DNA (mtDNA) between Pacific and Atlantic walruses found haplotype frequency differences among small samples from Northwest, West and East Greenland (Cronin et al. 1994). Subsequent studies of variation in mtDNA and nuclear DNA (microsatellites), using larger samples, have provided useful insights on population sub-structure of walruses in Greenland and neighboring areas (**Paper 8**; Andersen et al. 1998; Andersen & Born 2000; Andersen et al. 2004).

An analysis of 211 Atlantic walruses grouped them into four sub-populations: West Greenland, the North Water, East Greenland, and Svalbard-Franz Josef Land (**Paper 8**). Genetic distance and geographic distance between the sampling areas were significantly correlated ("isolation-by-distance effect"), especially at the mtDNA level. It was concluded that the genetic divergence observed at the nuclear level and especially at the mtDNA level between the North Water and the two eastern sub-populations (East Greenland and Svalbard-Franz Josef Land) most likely reflects pre- and post-glacial divergence (Ibid.). According to that hypothesis, the North Water and West Greenland areas would have been re-colonized from the west after the LGM and East Greenland would have been re-colonized by walruses that had survived the LGM in eastern Atlantic areas (see **Appendix I** section "The latest expansion into the Arctic").

Paper 8 and the studies by Andersen et al. (1998) and Andersen & Born (2000) did not include walruses from Canadian areas. However, a recent study (Andersen et al. 2004) that included 70 walrus samples from eastern and northern Hudson Bay, Hudson Strait and Ungava Bay (plus 48 additional samples from East Greenland) indicated that five sub-populations were represented (n_{total}=329): Eastern Hudson Bay-Hudson Strait, West Greenland, North Water, East Greenland and Svalbard-Franz Josef Land. Although the latter four sub-populations had been confirmed by earlier studies, the first was novel. The analysis also indicated that walruses in those parts of Canada and in West and Northwest Greenland probably once belonged to a single ancestral popu-

lation. Furthermore, the analysis indicated that walruses from the Hudson Strait area contribute to an unknown extent to the spring hunt off West Greenland. Such genetic evidence implies a direction of migration consistent with the suggestion by Freuchen (1921) and Vibe (1950, 1956a) (cf. **Paper 3** for a detailed discussion) of a large-scale counter-clockwise migration of walruses in the Baffin Bay region.

The walruses that occur in "West Greenland" south of Melville Bay likely belong to the "West Greenland stock" ("stock 4" in Born et al. 1995). However, based on distribution, timing of migration and catches, walruses wintering along the western coast of Disko Island and farther north may represent the southern extreme of the North Water sub-population, whereas those occurring farther south belong to the West Greenland sub-population (Born et al. 1995). Samples for genetic analysis are not available from the area between Disko Island and 76° N, and individual walruses have not been tracked in that area. Hence, no firm conclusion can be reached concerning the demographic affinities of the likely few walruses wintering in the shear zone along the coast between Disko Island and ca. 76° N.

Finally, an adult male walrus with a unique "Pacific walrus haplotype" was shot in Scoresby Sound in 1991, demonstrating that stragglers occasionally move over long distances (Andersen et al. 1998).

Satellite telemetry: During the last couple of decades, satellite telemetry has been used widely to study the movements of individual marine mammals (e.g. McConnell 1986; Fancy et al. 1988), and recently also to delineate sub-populations (e.g. Taylor et al. 2001).

The first walruses were instrumented with satellite transmitters in Alaska in 1987 (Harris et al. 1990; Hills 1992), followed in 1989 by deployment on Atlantic walruses in Greenland (**Paper 1**) and Svalbard (Wiig et al. 1996a).

After several unsuccessful attempts to immobilize walruses for deployment of satellite transmitters in the North Water pack ice in 1988, 1989 and 1991 (Born 1991; Born & Knutsen 1988, 1990a; Born unpubl.)

and off Sisimiut, West Greenland, in 1990 (Born unpubl.), a total of 12 male walruses were immobilized in 1989 and 1990 in Northeast Greenland (**Paper 1**; Born & Knutsen 1990b,c). In connection with a study of energy expenditure (Acquarone 2004), another 15 "tusk transmitters" were deployed on male walruses in Dove Bay (ca. 77° N; n=10) and at Sand Island in Young Sound (ca. 74° N; n=5) in Northeast Greenland (**Paper 11, 13**; Acquarone 2004; Table 2). Overall, the duration of contact with the animals averaged 87 days (SD=57 days; min-max: 4-238 days; median: 92 days; n=25) with no difference among years (F=1.253; p=0.316; 2 transmitters omitted because 1 animal died during re-immobilization and 1 transmitter was damaged during deployment). All instrumented walruses remained in the East Greenland area during the period of contact (**Paper 1, 11, 13**; Acquarone 2004; Born unpubl. data), supporting the conclusion of genetic studies that East Greenland walruses constitute a separate demographic unit.

A major obstacle to overcome in applying satellite telemetry to walruses is the difficulty of immobilizing them safely (Stirling & Sjare 1988). In most studies of free-ranging walruses, fast-acting opioid-like immobilization agents have been used. However, these can be fatal to both animals and researchers (Born & Knutsen 1990c; Hills et al. 1992; Griffiths et al. 1993, 2004; Lanthier et al. 1999; Mulcahy et al. 2003; Acquarone et al. 2004b). Hence, to avoid the complicating process of immobilization, satellite tags have been attached to un-restrained walruses in Alaska in recent years (J. Garlich-Miller, US Fish and Wildlife Service, pers. comm. 2004), and 4 tethered satellite tags (SPOT-4; Wildlife Computers) were deployed by the Greenland Institute of Natural Resources and the National Environmental Research Institute, on an experimental basis, on un-restrained walruses in Young Sound in August 2004 (Born & Dietz unpubl. data), Table 2.

Marking: Marks such as conventional tags (e.g. flipper tags, e.g. Kapel et al. 1998), natural external markings (e.g. tail fluke patterns; Hammond et al. 1990; Smith et al. 1999) and "genetic tagging" (e.g. Palsbøll et

al. 1997) can provide information on gross movements and site fidelity in marine mammals. Recaptures of walruses bearing flipper tags have provided information on gross movements and site fidelity in Greenland. For example, an adult male that had been tagged on 18 June 1989 at Anoretooq/Cape Inglefield (ca. 78° 30´ N) in Northwest Greenland was shot by a hunter on 17 May 1991 about 70 km south of the tagging site (Born 1991; Born et al. 1995), indicating site fidelity of walruses in the North Water.

Hunter-returned tags have also provided information on gross movements in East Greenland: An adult male (4349; Table 2) tagged in Dove Bay in August 2000 was shot at the entrance of Scoresby Sound on 15 June 2003. Another adult male tagged in Young Sound in late July 2001 (6482; Table 2) was shot at Scoresby Sound in May 2002 (Born upubl. data). This information on gross movements is in accordance with Andersen et al. (1998, 2004), who found that samples from Dove Bay, Young Sound and the entrance of Scoresby Sound did not differ genetically, and information in **Paper 6** in which photo-identification of individuals was used to demonstrate a connection between the haul-outs in Dove Bay and Young Sound. Hence, "tag" returns support the notion that walruses in East Greenland belong to one coherent sub-population.

There is, however, direct evidence of exchange between walruses in East Greenland and neighboring Svalbard. An adult male that was tagged in Dove Bay in 1989 was observed in northwestern Spitsbergen (Svalbard) in 1992 (**Paper 2**).

Other indications of population sub-structure: Regional variation in body size and in tissue levels of various chemical elements and compounds also indicate the existence of sub-populations of walruses in Greenland and Canada.

The asymptotic standard body length (SL) of male and female walruses from Northwest Greenland (North Water sub-population) was significantly larger than that of walruses from Hudson Bay but did not differ significantly from that of walruses from Foxe Basin (**Paper 4**; Garlich-Miller & Stewart 1998). Furthermore, walruses in

Table 2. Type of satellite transmitters deployed on walruses in Northeast Greenland (1989-2004) and their performance.

Year	Location	Satellite transmitter ID	Type	Day of instrumen- tation	Date of last uplink[1]	Number of days active
1989	Dove Bay [2]	4344	ST-3 [10]	9 Aug.	23 Aug. 1989	15
	Dove Bay [2]	4345 [7]	ST-3 [10]	12 Aug.	30 Nov. 1989	111
	Dove Bay [2]	4347	ST-3 [10]	13 Aug.	29 Oct. 1989	78
	Dove Bay [2]	1858	ST-3 [10]	14 Aug.	2 Oct. 1989	50
	Dove Bay [2]	1856	ST-3 [10]	19 Aug.	1 Oct. 1989	46
	Dove Bay [2]	1859	ST-3 [10]	24 Aug.	12 Sep. 1989	20
1990	Dove Bay [2]	4348	ST-3 [10]	6 Aug.	23 Nov. 1990	110
	Dove Bay [2]	4346	ST-3 [10]	7 Aug.	10 Aug. 1990	4
	Dove Bay [2]	4349 [7]	ST-3 [10]	8 Aug.	2 Apr. 1991	238
	Dove Bay [2]	3985	T-2028 [11]	11 Aug.	11 Oct. 1990	62
	Dove Bay [2]	3984	T-2028 [11]	12 Aug.	1 Dec. 1990	112
	Dove Bay [2]	1857	ST-3 [10]	19 Aug.	13 Jan. 1991	148
1999	Young Sound [3]	6481 [8]	ST-10 [12]	23 Aug.	21 Nov. 1999	91
2000	Dove Bay [4]	6480	ST-10 [12]	1 Aug.	12 Nov. 2000	103
	Dove Bay [4]	3985	ST-10 [12]	3 Aug.	7 Sep. 2000	36
	Dove Bay [4]	4349	ST-10 [12]	7 Aug.	12 Sep. 2000	44
	Dove Bay [4]	4346 [9]	ST-10 [12]	15 Aug.	27 Aug. 2000	13
	Dove Bay [5]	4347 [7]	ST-10 [12]	18 Aug.	4 Mar. 2001	199
	Young Sound [4]	11274 [8]	ST-10 [12]	27 Aug.	27 Aug. 2000	0 [13]
2001	Young Sound [4]	4344 [8]	ST-10 [12]	24 Jul.	5 Oct. 2001	92
	Young Sound [4]	11272	SPOT-2 [12]	27 Jul.	26 Nov. 2001	124
	Young Sound [4]	6482	SPOT-2 [12]	28 Jul.	19 Nov. 2001	116
	Dove Bay [4]	6483	SPOT-2 [12]	3 Aug.	3 Dec. 2001	124
	Dove Bay [5]	11271 [7]	SPOT-2 [12]	6 Aug.	21 Aug. 2001	16 [14]
	Dove Bay [4]	6480	SPOT-2 [12]	7 Aug.	6 Dec. 2001	122
	Dove Bay [4]	11273 [9]	SPOT-2 [12]	10 Aug.	14 Oct. 2001	77
	Dove Bay [4]	11274	SPOT-2 [12]	18 Aug.	25 Sep. 2001	40
2004	Young Sound [6]	52060	SPOT-4 [12]	3 Aug.	31 Aug. 2004	29 [15]
	Young Sound [6]	52061	SPOT-4 [12]	7 Aug.	11 Aug. 2004	5 [15, 16]
	Young Sound [6]	52062	SPOT-4 [12]	7 Aug.	27 Aug. 2004	19 [15]
	Young Sound [6]	52063	SPOT-4 [12]	9 Aug.	18 Aug. 2004	10 [15, 17]

1: Uplink=last contact between transmitter and satellite; 2-6: Source; 2: **Paper 1**, 3: **Paper 11**; 4: Born & Acquarone unpubl.; 5: **Paper 13**; 6: Born et al. unpubl.; 7-9: indicate that the same (three) animals were tracked in different years; e.g. 7) was tracked during 4 years, **Paper 13**; 10-12: Manufacturer; 10: Telonics, 11: Toyocom, 12: Wildlife Computers; 13: Unit cracked during deployment; 14: Died during a second immobilization that same season; 15: These tethered satellite tags were not included in the summary statistics (text); 16: was observed at the haul-out on 12 Aug. with the transmitter attached, observed again on 16 Aug. without it; 17: The transmitter was shed at the haul-out on 18 Aug. Two ST-6 transmitters that were deployed on adult males in Young Sound, August 1994, (Born & Wiig 1995) did not transmit after deployment and are not included here.
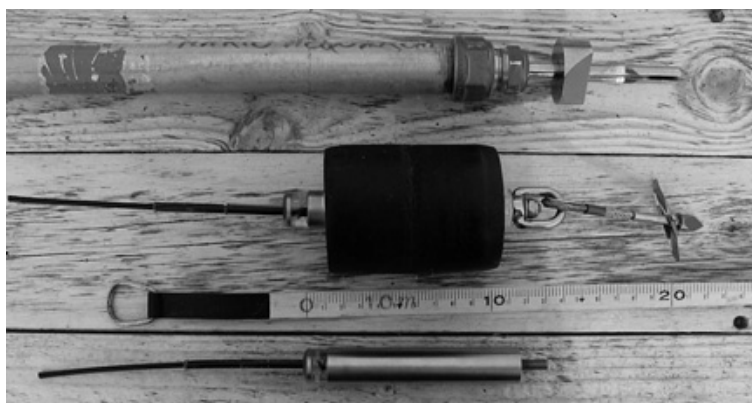
Photo 4. A SPOT-4 tethered satellite tag that was used by the Greenland Institute of Natural Resources and the Danish Environmental Research Institute for tracking walruses in Northeast Greenland in 2004. The tip of the pole that was used to attach the transmitters to the animals is seen above the transmitter.
Photo: M. Acquarone.

Foxe Basin were larger than those in Hudson Bay (Mansfield 1958; Garlich-Miller & Stewart 1998). Data from West and East Greenland were not sufficient to include those areas in the analyses of regional variation in body size (**Paper 4**).

Outridge et al. (2003) compared lead (Pb) ratios in teeth of walruses sampled in several areas of Canada and Greenland. Although some overlap of Pb-ratio values existed, significant differences were found among several sampling sites. Of direct relevance in the present context were indications of differences among walruses from West Greenland, Northwest Greenland (the North Water), southeastern Baffin Bay (only 4 specimens) and eastern Hudson Bay (i.e. "stock 3"; Fig. 3). Furthermore, walruses from Scoresby Sound differed from walruses in West and Northwest Greenland (Ibid.). Within the North Water sub-population, ca. 80% of the animals landed in the Qaanaaq municipality in Northwest Greenland and ca. 20% of those landed at Grise Fiord on Ellesmere Island had dissimilar signatures, indicating some sub-structuring of the North Water sub-population (Outridge et al. 2003). Some sub-structuring in the North Water sub-population was also indicated in the genetic study by Andersen & Born (2000) whereas de March et al. (2002) did not find differences between walruses from Grise Fjord in Jones Sound and Resolute Bay/ Bathurst Island (i.e. within the western range of the North Water sub-population). Hence, although not easy to interpret, the Pb-ratio data basically support the existence of three walrus sub-populations in Greenland but also indicate some further structuring within these sub-populations.

Organochlorine (OC) levels and patterns differed regionally among samples of walruses from Canada and Greenland (Muir et al. 2001). Walruses from East Greenland had higher levels of certain OCs (PCBs, DDTs) than walruses in Northwest Greenland (no samples from West Greenland). Furthermore, there were indications that walruses from Loks Land on southeastern Baffin Island differed in patterns and levels of OCs from walruses from the North Water (Ibid.).

It must be added that walruses have been observed in southern Baffin Bay/ northern Davis Strait (i.e. between West Greenland and southeastern Baffin Island), and that the waters off Central West Greenland are devoid of walruses during summer (**Paper 3**). Hence, the walruses that winter in Central West Greenland summer in adjacent areas that apparently do not include the North Water and/or the Hudson Strait regions as indicated by the genetic studies (Andersen et al. 1998, 2004; submitted; Andersen & Born 2000; **Paper 8**). Likely, West Greenland walruses spent some period of the year along eastern Baffin Island. However, except for this "West Greenland-Baffin Island" connection, Atlantic walruses have apparently become more sedentary than in the past, when they were much more abundant in the Atlantic Arctic (Mansfield 1958, 1973; Born et al. 1995).

In conclusion: Three sub-populations of walruses are found in Greenland (North Water, West Greenland and East Greenland). The North Water and East Greenland sub-populations inhabit areas with high-Arctic conditions, whereas the West Greenland sub-population ranges into sub-Arctic waters.

These sub-populations may have developed as a response to either: (1) relatively small population size or, more likely, (2) the necessity of wintering in areas with predictable food, "open" water and access to mates. The physical conditions (bathymetry and ice conditions) along the Greenland coasts likely also form barriers to movement between the three walrus sub-populations. The walruses living in East Greenland are isolated from those on the western coast by the heavy pack ice lying close to the coast of northern Greenland and in the south by long stretches of coast in southeastern and southwestern Greenland with no apparently suitable walrus habitat (**Paper 8**). During winter the Baffin Bay pack ice lies close to the coast of Greenland between Disko Island and the North Water. Furthermore, along this stretch of coast there are few banks with suitable walrus habitat.

Hence, the status of walruses in the three Greenland areas must be evaluated separately.

Abundance in Greenland

Walrus numbers are difficult to estimate because the animals are distributed over vast areas. This usually results in low sampling effort and means that sampling surveys often need to be spread across a number of days. Furthermore, the animals tend to occur in clumps, large groups are difficult to count because individuals often lie close together, an uncertain fraction is in the water and either diving (and thus invisible) or easy to miss, and their cryptic coloration can make walruses hard to detect whether in the water or on land (Estes & Gilbert 1978; Gilbert 1999; Udevitz et al. 2001).

Basically, two options are available for counting walruses: (1) aerial surveys when they are distributed offshore in areas with pack ice, or (2) counting them at terrestrial haul-outs during late summer and fall (Gilbert 1999 and references therein). A third option would be mark-recapture estimation, but this method has been judged infeasible for estimating abundance of Pacific walrus, because too much effort would be needed to mark and recapture a sufficiently large sample of animals (Anon. 2003). A mark-recapture estimate was made, however, for

a small group of Atlantic walruses at the Sand Island haul-out in Young Sound in 2002-2003 (Born et al. unpubl.).

Walruses no longer haul-out on land in West and Northwest Greenland (**Paper 3**; Born et al. 1995; see section "Change in distribution"). Hence, they can only be counted in the pack ice during spring (West Greenland) or when they are at terrestrial haul-outs in Canada during summer (North Water population).

Counts need to be adjusted for animals out of sight during the surveys either because they were submerged in the water or away from the haul-out site on foraging excursions. Satellite-linked dive-recorders and time-depth recorders have provided information on walrus diving and haul-out behavior (**Paper 1, 5, 9, 11, 13**; Hills 1992; Wiig et al. 1993; Jay et al. 2001; Gjertz et al. 2001). During summer, walruses generally spend about 30% of their time hauled out, and when at sea they spend about 80% of their time submerged. These crude estimates were used to correct aerial survey counts of walruses in the West Greenland and North Water sub-populations (**Paper 12**).

West Greenland: Line-transect aerial surveys flown during spring in the early 1990s were used to estimate the number of walruses wintering in West Greenland (**Paper 3**). Based on these surveys, the number of walruses wintering off West Greenland was estimated at ca. 1000 (**Paper 12**). This estimate included a correction based on activity data obtained from SDRs deployed in Northeast Greenland (**Paper 1, 5, 9, 11**) to account for haul-out and diving activity.

Whereas the North Water and East Greenland sub-populations likely represent distinct population units, the demographic identity of walruses wintering in West Greenland remains uncertain. They may or may not represent a demographically distinct unit (see section "Identifications of sub-populations of walruses"). However, in **Paper 12** the impact of hunting removals on this sub-population was modeled using the precautionary assumption that walruses wintering in Central West Greenland constitute a distinct population unit. Inevitably, the result of an evaluation of the status of West Greenland walruses will be affected by

this assumption. The alternative assumption, that walruses off West Greenland are part of a population with a wider range that includes eastern Baffin Island, may give a less worrisome result. However, in the absence of current information on the number of walruses along eastern Baffin Island, it is impossible to investigate the implications further at this stage.

The North Water: Since 1976 several attempts have been made to estimate the number of walruses in the North Water sub-population. However, information on numbers of walruses in the North Water and adjacent areas has been collected in different seasons and in different years. Both aerial surveys and ship-borne surveys have been used and the entire range has not always been covered. The results were reviewed by Born et al. (1995), who suggested that the North Water sub-population numbered approximately 1700-2000 walruses (and perhaps as many as 3000).

In order to estimate the North Water sub-population, aerial surveys were flown over important Canadian summer distribution areas in 1999 (Dunn 2000). The counts, corrected for walruses not seen (i.e. at sea and/or submerged), resulted in an estimate of ca. 1000 walruses (**Paper 12**). However, to account for walruses potentially present in unsurveyed areas, another 500 animals was added, and furthermore it was suggested that the estimate of 1500 probably was negatively biased (Ibid.).

East Greenland: Systematic walrus surveys have not been conducted in East Greenland. Based on several observations since 1980, Born et al. (1997) estimated that the East Greenland sub-population numbered 500-1000 and suggested that the high end of that range was probably more realistic. **Paper 12** used a current abundance estimate of 1000 to model trends in this sub-population.

Socio-economic development and walrus catches in Greenland

Socio-economic developments

The scope and intensity of walrus hunting in Greenland waters reflected socio-eco-

nomic factors first in Europe (exploitation of marine mammals overseas by the Netherlands, Britain, Norway and Denmark) and then in Greenland. Changes in patterns of exploitation in Greenland result from the interactions among climate, ecological processes, and socio-economic factors, as shown in the West Greenland "cod-to-shrimp" transition during the 20th century (Hamilton et al. 2003). Socio-economic changes, particularly during the 20th century, had major implications for the exploitation of walruses in Greenland.

Prior to the 19th century, walruses were taken by Greenlanders (e.g. Gad 1970; Rink 1877; Gulløv 2004), Norsemen (from 985 until the latter half of 1400) (e.g. Gad 1970; Roesdahl 1995; Gulløv 2004), and European whalers, sealers and explorers (from the 17th century until 1923) (e.g. Peary 1903, 1910; Gad 1973; Ross & MacIver 1982; Fosheim 1994). However, the information on catches during these periods is generally inadequate. Furthermore, the sources are scattered and in many cases inaccurate as to numbers taken and locations. Hence, I have considered it beyond the scope of this study to review in detail the catch history of walruses prior to the 20th century. This decision is further justified by the fact that it was not until the beginning of the 20th century that demographic and technological developments in Greenland changed dramatically in ways that would have great consequences for the exploitation of living resources (e.g. Mikkelsen & Sveistrup 1944; Andersen 1998), including walruses (**Paper 3**). Such developments coincided with increases in air and water temperatures (e.g. Førland et al. 2003) that markedly changed the composition of the marine fauna of western Greenland (Jensen 1939).

The population of Greenlanders increased steadily from a total of ca. 6000 in 1805 to ca. 13500 in 1921. Then the population increased at a slightly higher rate, reaching ca. 20500 in 1948, after which time the growth rate increased markedly. In 1998, the population of Greenlanders (i.e. excluding people born outside Greenland) numbered ca. 49000 (Marquardt 2002). Within historical time, the population has concentrated in southwestern and western

Greenland (north to ca. 72° N) where the conditions for marine productivity are comparatively favorable (e.g. Born 2001).

Until the 1920s, the hunt for pinnipeds (five species) constituted the mainstay of the Inuit society in Greenland (e.g. Andersen 1998; Marquardt 1996, 1999, 2002). This hunt provided the Greenlanders with food, fuel, skin for making clothes and boats (kayaks and umiaks, i.e. large boats for transport) – and quite importantly also with blubber that could be traded to the Royal Greenland Trade Department (KGH=Den Kongelige Grønlandske Handel) and then exported as train oil (e.g. Andersen 1998). Walruses played a role in this economy. In addition to providing the Greenlanders with food for local consumption and ivory for making tools (e.g. Gad 1970), the blubber and the tusks were traded to KGH, which maintained an effective trade monopoly until 1950 (e.g. Vibe 1967; Gad 1970, 1973).

Throughout the first half of the 19th century, international train oil prices were high because demand was strong and supply was diminishing because of a general reduction in the catch of whales. However, from the 1860s, train oil met growing market competition from mineral oil products and prices on train oil decreased nearly 50% between 1861-1870 and during the first decade of the 20th century (Hammer 1921; Thorleifsen 1999). Prices increased somewhat in 1916-1918 (Hammer 1921) but a further drastic decrease in the international prices of train oil occurred between 1924 and 1932 (Sveistrup 1950). Nevertheless, the amount of blubber traded to KGH continued increasing steadily until 1910, when world market prices on salted fish surpassed that of train oil (Ibid.). Although seal skins could be sold on the European market during the late 19th century (e.g. Marquardt et al. 1999), the numbers of seals caught and skins traded in Greenland decreased from around 1910 (e.g. Anon. 1947, 1950). Overall, the net value of Greenland's *per capita* production decreased about 20% from 1845-1910 (Gad 1950). However, prices paid by KGH for Greenland hunting products did not reflect world market prices. Rather, prices were set at levels

intended to secure steady incomes for Greenlanders (Sveistrup 1950).

The Greenland economy changed during the 1910s and 1920s from being primarily hunting-product based to being primarily fishery-product based (for details about this transition see Boisen & Nielsen 1982; Sørensen 1982; Smith 1983). Among the factors responsible for this transition were: 1) socio-economic trends (e.g. reduced world market prices on train oil, increased prices for salted fish, and human population growth), (2) a general decrease in numbers of seals taken in Greenland (in case of harp and hooded seals, this decrease was likely caused by over-exploitation elsewhere by foreign sealers; e.g. Mikkelsen & Sveistrup 1944; Anon. 1950), and (3) a general warming that changed marine ecosystems and most notably brought the boreal Atlantic cod to western Greenland (Jensen 1939).

Photo 5. A female walrus and her newborn calf have been brought back from a hunting trip to the "West Ice" and are about to be butchered in Sisimiut (West Greenland) (probably 1935). A relatively large fraction of the walruses taken in West Greenland was females (**Paper 3, 12**).
Photo: A.C. Rasmussen (Sisimiut Museum).

West Greenland: The aforementioned socio-economic change, including changes in technology, had a marked effect on the exploitation of walruses in West Greenland. Of greatest importance was the introduction of motorboats (**Paper 3**; Photo 5). In Central West Greenland, motorboats were used not only for fishing, but also to catch marine mammals (walruses, beluga whales, *Dephinapterus leucas*, and bearded seals, *Erignathus barbatus*) in the eastern edges of the West Ice (**Paper 3**; Anon. 1950), Photo 5, Fig. 7. Motorboats radically extended the operational range of the hunters and reduced their dependence on good weather (e.g. Andersen 1998). They also greatly enhanced the hunters' ability to navigate in the pack ice areas where walruses were found. From 1924, the KGH began to sell motorboats to Greenlanders (who could buy them on interest-free loans), and from 1924 until 1939 the number of motorboats (typically 20-22 feet, Anon. 1950) owned by West Greenlanders increased from 2 to 72 (Rask 1993; Andersen 1998). Of a total of 72 motorboats owned by West Greenlanders in 1939 (excluding the Qaanaaq area in Northwest Greenland), 58% (42) were stationed in the Sisimiut-Disko Island area (Rask 1993) where the West Greenland sub-population of walruses was hunted (**Paper 3**). This percentage had increased to 72%

(93 of 129 boats; Qaanaaq with 1 boat excluded) by 1946/47 (Anon. 1950).

In the important walrus hunting town of Sisimiut, a new socio-economic and technical era began in the mid 1920s with the establishment of a fish-processing plant, followed by investment in privately owned motorized fishing vessels and a local shipyard (Hamilton et al. 2003).

Walrus ivory, hide (for machinery belts etc.) and blubber (train oil) could be traded to the KGH (**Paper 3**). Despite difficulties with selling walrus hides on the European market and a drop in international train oil prices in the 1930s, the trade in walrus hides and blubber from West Greenland remained high (Ibid.).

In addition to the hunting activity, the disturbance caused by an increased fishery since World War II at and along the West Greenland banks likely have negatively influenced on the walruses in this area (Fig. 8).

Socio-economic development in Northwest and East Greenland during the late 19th and 20th centuries differed from that in West Greenland.

Northwest Greenland: Formally, Northwest Greenland (i.e. the Qaanaaq municipality or "Thule area or district") did not come under Danish administration until 1936 (e.g. Holtved 1950) and technical development in this area generally came later than in West

Fig. 7. The reported catch of walruses in West Greenland, 1900-2002 (sources: **Paper 3** and **12**; for 2000-02 "Piniarneq", the new system of reporting the catch that was introduced in 1993).
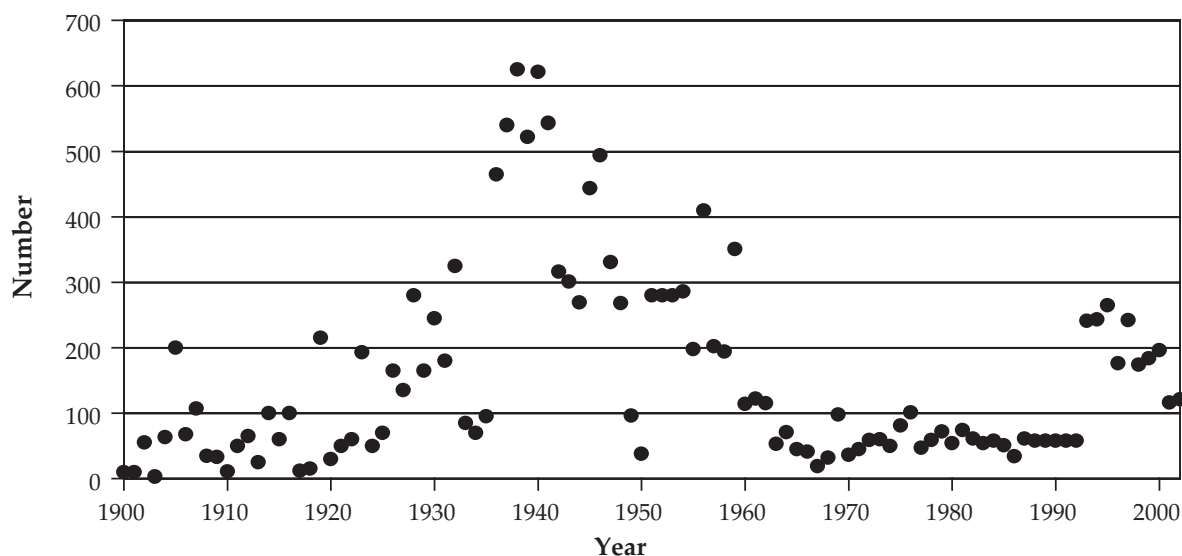
Greenland to the south (e.g. Rasmussen 1921; Gilberg 1976). Until after World War II, there was only one motorboat in the area (Andersen 1998). This schooner, belonging to the trade station at Dundas (Pituffik/Thule Air Base), was engaged in walrus hunting in the Appat/Saunders Island area early in the 20th century (Freuchen 1921). According to Holtved (1967), the two (*sic*) motorboats of the trade station were used to transport the hunters to and from the walrus hunting grounds during 1935-37 and 1946-47. At this time, "open-water" hunting of walruses was still conducted mainly from kayaks but also to a limited extent from motorboats. From the 1960s, motorized boats were increasingly used during the hunt for walruses.

The Inuit living in Canada on the western side of the North Water also hunted walruses from this sub-population. However, it is likely that, given the low numbers of Inuit living in the eastern Canadian High Arctic, the traditional catch of walruses there was not very large. However, as trading posts and police detachments became established during the first half of the 20th century, the removals of walruses on the Canadian side increased (Born et al. 1995 and references therein). Furthermore, establishment of the Grise Fiord Inuit community on the northern coast of Jones Sound in the mid 1950s (Riewe 1977) increased the catch of walruses from the North Water sub-population (**Paper 12**; Born et al. 1995).

East Greenland: Historically, the Inuit who lived in small groups scattered along the eastern coast of Greenland caught walruses, as evidenced by finds of walrus bones in house ruins and mittens (e.g. Mikkelsen 1950). The last group of Inuit in Northeast Greenland was encountered in 1822, and until 1924/25 this coast was populated only by the Inuit living in the Ammassalik area south of ca. 68° N (Ibid.).
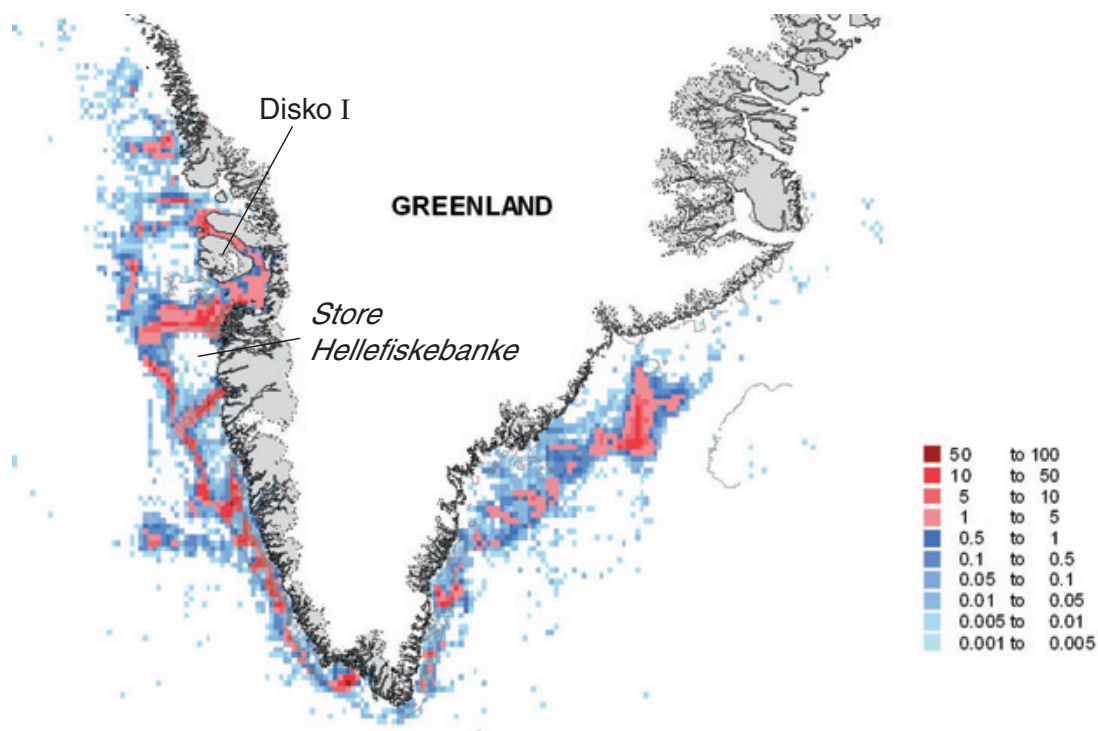

Fig. 8. Since World War II, there has been an increased fishery in West and Southeast Greenland. In particular, this fishery has concentrated at (cod) and around (shrimp) the shallow banks in West Greenland where walruses winter. It cannot be excluded that noise from this activity and disturbance of the bottom fauna have negatively influenced on the walruses in the area. Potential habitat degradation caused by fishery has not been assessed in Greenland. The graph reflects the degree of disturbance by fishery during the last 20 years based on records in log-books in the shrimp, cod, Greenland halibut and scallop fishery. Legend: Number of times a m² has been fished. Source: Rikke Frandsen (Greenland Institute of Natural Resources).

A trade and mission post was established in this area in 1894 (Mikkelsen 1950). The East Greenland Inuit population numbered less than 500 in the late 19th century but had increased to ca. 1100 by 1938 (Mikkelsen & Sveistrup 1944). However, more importantly from a "walrus catch" point of view, walruses occurred (and still occur) only irregularly and sparsely in the Ammassalik area (**Paper 6**). Therefore, they have never been quantitatively important as game animals in Southeast Greenland (Mikkelsen & Sveistrup 1944). The situation changed when, in 1924/25, a group of Inuit from Ammassalik settled at the entrance of Scoresby Sound (Mikkelsen & Sveistrup 1944) where walrus haul-out site was in Hvalrosbugten, very close to the settlement of Ittoqqortoormiit/Scoresbysund (**Paper 6**). During the first years after the community had been established, the catch of walruses was relatively high. However, the local group of walruses either was quickly exterminated or learned to avoid the area (Ibid.).

Of even greater consequence to the East Greenland walrus sub-population was the incursion by foreign sealers and trappers in areas north of Scoresby Sound between 1889 and the late 1950s-early 1960s. During that period, the walrus population was heavily exploited, and by the 1950 there were signs that it had been severely decimated in areas south of ca. 77° N (i.e. the areas frequented by the sealers and trappers). In 1956, hunting regulations were introduced in Northeast Greenland and by the establishment in 1974 of the "National Park of North and Northeast Greenland", walruses became fully protected within the major part of their range in East Greenland (**Paper 6**).

In summary: In West Greenland, marked changes in strategies and means of exploitation of living resources, driven by climatic and socio-economic factors, led to increased catches of walruses during the first half of the 20th century. The authorities subsidized this increased exploitation economically and thereby sustained a high hunting effort. In Northwest Greenland, the relevant socio-economic changes, including increased use of motorized vessels for hunting, were not triggered until the 1960s. During a brief period in the mid 1920s, walruses were numerically important game for the Inuit living at the entrance of Scoresby Sound. More importantly, between 1889 and the 1950s foreign sealers and heavily taxed the walrus population in Northeast Greenland.

The catch of walruses

Paper 3, 6 and 12 present data on the catch of walruses in Greenland. However, in many cases, information was inadequate and it was necessary to estimate the catches by both Greenlanders and foreigners (Ibid.).

West Greenland: Reported catches in West Greenland increased from 1900 until 1936-1941, when an average of 553 walruses were secured annually (losses not included in this and other figures given in this section). The catch in this area then decreased drastically (**Paper 3, 12**). After 1993, when a new system of reporting catches was introduced ("The Piniarneq"), the reported annual catch of walruses (loss not included) increased from an estimated average of 62 during 1960-1992 to 196 during 1993-2002 (This study; **Paper 12**); Fig. 7.

The North Water: The catch from the North Water population is not well documented (**Paper 12**). Between 1960 and 1992 the estimate of the annual catch by Greenlandic and Canadian Inuit was ca. 180 walruses; for the period 1993-2002 the estimate of the catch averaged 145 walruses per year. In 1949 and 1951, foreign sealers took substantial numbers of animals from this sub-population (This study; Born et al. 1995**; Paper 12**).

East Greenland: The catch of walruses in southeastern Greenland has always been negligible (Mikkelsen & Sveistrup 1944; **Paper 6**). However, catches in East Greenland increased markedly in the decades after 1889, when a European sealer managed to penetrate the pack ice in the Greenland Sea and reached the "pristine" hunting grounds in northeast Greenland (Born et al. 1997). The hunt of walruses in East Greenland by foreign sealers and trappers ceased in the 1950s.

Since the introduction of walrus hunting

regulations in Greenland in the 1950s (Born et al. 1995), only Greenland citizens have been allowed to hunt walruses. Between 1956 and 1992 the annual catch of walrus was 4; the reported catch during 1993-2002 averaged 8 walrus per year (This study; **Paper 6, 12**).

There are no quotas, and never were any, for the catch of walruses in Greenland (see section "Regulation of the hunt").

Effects of catches

Effects on numbers

The historical trends and projected future trends for the walrus sub-populations in Greenland were examined using Bayesian methods and an age- and sex-structured model (**Paper 12**). Input to the model included: (1) catch data, and estimates of (2) hunting loss, (3) current abundance and (4) vital parameters (adult and juvenile survival, maximum birth rate, age of reproductive maturity of females). The analysis indicated that the West Greenland and North Water sub-populations were over-exploited during the 20th century and that their current abundance is only a few percent of historical abundance. Apparently, both of these sub-populations are still being exploited above sustainable levels.

Since protective measures were introduced in the 1950s, the East Greenland sub-population, which has its main distribution in unpopulated areas where it is protected, likely has increased to near its pre-exploitation abundance. The present exploitation of this sub-population appears sustainable.

Catch and temperature

The reported catch of walruses (i.e. annual catch figures indexed to the largest annual catch during the period under consideration) from the West Greenland sub-population was significantly positively correlated with the annual mean temperature measured at Nuuk (only station available with a long data series) during the period 1900 to 2002 (r=0.27; z=2.76; p=0.006; n=103 years). Hence, the catches increased during the period with increased temperatures. Similar statistically

significant correlations between catch and temperature were not found for either the East Greenland (Tasiilaq temperatures vs. catches during 1895-1999: r=-0.03; z=-0.30; p=0.77; n=105) or the North Water sub-population (Pituffik/Thule Air Base 1948-1999: r=-0,14; z=-1,00; p=0.31; n=52). It must, however, be kept in mind that catch statistics from the East Greenland and North Water sub-populations are far from complete.

Although I realize that a correlation between two sets of data does not prove that there is a causal relationship between them, I suggest that in this case, warming and decreased ice cover made walruses in West Greenland more accessible to hunters in motorized vessels in (see sections "Socio-economic developments", "Sea ice" and "Evalution").

Change in distribution

During the last ca. 100 years the distribution of walruses in Greenland has changed.

West Greenland: In West Greenland, large numbers of walruses formerly hauled out on *uglit* situated on small islands and on the mainland coast between approximately 67° 25' N and 67° 47' N. Walruses rarely frequented those *uglit* after the late 1930s, and since the early 1950s there have been no reports of walruses hauled out on land in this region. Undoubtedly, it was hunting at the *uglit* that caused walruses to abandon them. Farther north in the Disko Island area and in the Upernavik area at ca. 73° 10' N, other *uglit* were also abandoned in historical times (**Paper 3**).

Furthermore, walruses apparently arrived earlier in the fall in the central parts of West Greenland and disappeared later in the following spring than they do nowadays. In recent times, walruses reportedly arrive in October-November and leave sometime in May, as opposed to the first half of the 20th century when they arrived in August and remained until June-July. This change in migration pattern likely reflects an increase in duration of the period with a vessel-based hunt in West Greenland (**Paper 3**).

The North Water: Walruses no longer use

terrestrial haul-outs on the Greenland side of the North Water and in this region they now rely entirely upon access to *uglit* in the Canadian High Arctic (Born et al. 1995). Furthermore, the current absence of walruses in the eastern parts of the North Water area during summer is in contrast with the past situation when walruses sometimes occurred abundantly there during the open-water season (Born et al. 1995). Besides this decrease in the length of time that walruses spend in the Qaanaaq municipality, their geographical range during summer has also shrunk. Previously they occurred farther east in Wolstenholme Sound (i.e. close to Pituffik/Thule Air Base) and also penetrated McCormick Fjord between Siorapaluk and Qaanaaq (Vibe 1950; Born et al. 1995). Such changes were most likely caused by increased hunting from motorboats during the open-water season that lasts until sometime in October (Born 1987).

Overall, walruses appear to have been more numerous and more widely distributed in the Baffin Bay-Davis Strait area during the first half of the 20th century (**Paper 3**). Loughrey (1959) and Mansfield (1973) suggested that Atlantic walruses had more sedentary habits than Pacific walruses, and Mansfield (1973) questioned whether the large-scale, counter-clockwise migration cycle in the Baffin Bay-Davis Strait area suggested by Freuchen (1921) and Vibe (1950) actually occurred any more. Mansfield (1973) also indicated that walruses apparently had become scarce along the northeastern coast of Baffin Island.

Indications that walruses no longer migrate southward in significant numbers along either the northeastern coast of Baffin Island or the northwestern coast of Greenland can be interpreted to mean that they occur in more sedentary groups nowadays, and that their numbers have decreased substantially (**Paper 3**).

East Greenland: In East Greenland, haul-outs at the entrance of Scoresby Sound were permanently abandoned around the mid 1920s due to hunting by Inuit. Furthermore, due to hunting by foreigners, *uglit* in Young Sound and the Kuhn Island-Shannon Island area were abandoned at the beginning of the 20th century (**Paper 6**).

2

Part 2 – Food consumption and the effects of climate

In this section of the thesis, I review the information on benthic food for walruses in Greenland and summarize the studies to determine the food consumption of walruses. Furthermore, I attempt to evaluate whether there is enough food for them in Greenland. The temperature and ice conditions in Greenland since the early 1800s are summarized and the potential effects on walruses of climatic changes are discussed.

Food and energy requirements of walruses

Fay et al. (1977) estimated that a population of 200000 Pacific walruses would eat the standing stock of clams in the Bering and Chukchi Seas at a rate of 20% per year. The effects on walrus populations of removals by human hunters and of climatic fluctuations cannot be assessed without considering the carrying capacity of their food resources. A population of walruses approaching carrying capacity will itself have an adverse effect on its food supply, as was suggested for Pacific walruses in the late 1970s and early 1980s (Fay et al. 1989). A persistent change in the primary production regime caused by climate-induced changes in sea ice cover could lead to changes in species composition and standing stocks of the Arctic benthos (Klages et al. 2004).

Recent walrus studies in East Greenland have focused on determining the food consumption and energy requirements of individual walruses and the role of walruses in the marine ecosystem (**Paper 9, 11**; Acquarone 2004). In this section, I review information on biomass and productivity of benthic organisms, primarily the bivalves, in "walrus areas" off Greenland. Based on this information, combined with estimates of individual food consumption, I attempt to estimate the amount of food available to walruses in Greenland. My purpose is to gain an impression of the order of magnitude of the carrying capacity of walrus habitats in Greenland in relation to estimates of current sub-population sizes.

Densities and biomass of benthos

Generally, studies to determine benthic biomass and productivity in Greenland have been scattered both spatially and temporally.

West Greenland: Off the southwestern coast of Disko Island, average total wet weight (ww) biomass of *Serripes, Cardium, Macoma, Hiatella* and *Mya* at <100 m depth was ca. 679 g/m^2 and annual somatic production was ca. 99 g/m^2 (Petersen 1978). *Serripes* and *Mya* constituted ca. 78% of the biomass and were responsible for ca. 74% of the production. In Kangerluk/Diskofjord on the western coast of Disko Island, total biomass of invertebrate benthos (mollusks, echinoderms and polychaetes) averaged ca. 85 g/m^2 ash-free dry matter (Schmid & Piepenburg 1993), which corresponds to ca. 330 g ww/m^2 (conversion factor from dry matter to ww=3.9; **Paper 9**).

Farther north in the Upernavik area at ca. 72° N, the total average ww of the *Macoma*-community, which mainly constituted *Macoma, Mya* and *Hiatella*, was 160-388 g ww/m^2 (Vibe 1939). In this area, average benthic biomasses as high as 1482 g ww/m^2 were found locally (Vibe 1939), although such levels were considered exceptionally high (Vibe 1950).

The sources cited above indicate that average biomass of suitable walrus food in West Greenland ranges between ca. 150 and ca. 650 g ww/m^2 (mean: 400 g ww/m^2). It must be emphasized, however, that no extensive systematic surveys to determine distributions and densities of the bivalve benthos have been conducted on the banks where walruses concentrate during winter

(i.e. "Store Hellefiske Banke" and west of Disko Island). Hence, the carrying capacity of benthic food for walruses in West Greenland cannot be estimated with much certainty.

Northwest Greenland (the North Water): Average benthic biomass at Savissivik (southeastern North Water area) was 52 g ww/m² (Vibe 1950). Average biomass of the benthos was 160 g ww/m² in the Saunders Island area (Vibe 1939) and ca. 450 g ww/m² on the walrus foraging bank farther north in Murchinson Sound; bivalves constituted ca. 53% by weight (Vibe 1950). This indicates that the average biomass of walrus food in the North Water ranges between ca. 150 and ca. 450 g ww/m² (mean: 300 g ww/m²).

East Greenland: Benthic biomass has been reported to be 623 g ww/m² in the inner fjords of the Ammassalik area (Berthelsen 1937). In the Kangertiitivaq/Scoresby Sound and Kejser Franz Joseph Fjord areas, the total biomass of the *Macoma*-community was 100-200 g ww/m² (Thorson 1933; Ockelmann 1958). According to Thorson (1933), densities of the benthic invertebrate fauna of 350 g ww/m² were found at 10 m depth at the entrance of Scoresby Sound, whereas density in the inner parts of this sound and in Kejser Franz Joseph Fjord were only about 1 g ww/ m². The combined shell-free ww biomass and annual production of *Mya* and *Hiatella* at depths between 0 and 60 m in Young Sound were ca. 78 g ww/m² and 7.9 g/m² * year, respectively (Sejr 2005). In this fjord, the highest biomass was found in waters <35 m deep (Sejr et al. 2000). Hence, the estimated average biomass of walrus food in East Greenland ranges between ca. 100 and ca. 620 g ww/m² (mean: ca. 350 g ww/m²).

Individual food consumption

The food consumption and energy intake of free-ranging walruses were studied in Northeast Greenland during 1999-2001 (**Paper 9, 11**; Acquarone 2004). The main objectives were to: (1) determine individual food requirements and energy expenditure, and (2) estimate the impact of walruses on their benthic prey in a High Arctic marine ecosystem. The aim was to provide baseline data on the trophic role of walruses so that future changes caused by global warming could be monitored.

By combining underwater observations of feeding with satellite-telemetry data on movement and diving activity, the estimated daily consumption of bivalve wet matter corresponded to ca. 5% (95% CI: 3.3-5.9%) of walrus TBM (**Paper 9**). That estimate included time hauled-out. If, however, only time at sea was considered, the intake was ca. 6% of TBM (95% CI: 4.4-7.8%) (Ibid.). These estimates of daily food intake of free-ranging walruses were higher than daily food intake reported by Fisher et al. (1992) and Kastelein et al. (2000) for captive walruses but consistent with predictions by Fay (1982) for walruses in the wild and with daily consumption rates previously used to calculate walrus predation in the wild (Welch et al. 1992; Weslawski et al. 2000).

Field metabolic rate (FMR) was determined by use of double-labeled water in adult male walruses in Northeast Greenland in 2001. The resulting estimates of FMR in a 1370 and a 1250 kg male were 328 MJ/d and 365 MJ/d, respectively (Acquarone et al. 2004a). If the energy obtained from the FMR study were converted to "bivalve equivalents," it would correspond to ingestion of 5-6% of TBM mass per day (Acquarone 2004). The calculations in **Paper 9 and 11** involved only the bivalve component of the benthos. Hence, the estimates of individual food consumption based on direct observation did not take into account that walruses also consume other benthic invertebrates that do not leave traces on the sea floor after consumption.

The similarity of the estimates of individual food consumption obtained from the two different methods indicates that a daily *per capita* food ingestion during summer around 6% of TBM is plausible.

Based on movement and activity of individual walruses and estimates of individual food consumption, the predation by walruses on bivalves in Young Sound in East Greenland was quantified (**Paper 11**). It was estimated that 60 walruses consumed ca. 100 tons of clam soft parts during the open-water season (90 d). This estimate

Photo 6. In Young Sound (East Greenland), scuba divers collected the newly emptied bivalve shells from places where walruses had recently been feeding. The amount of clam meat that had been consumed during each dive was then determined in the laboratory (**Paper 9**). *Photo: G. Ehlmé/S. Rysgaard.*

amounts to ca. 2.5% of the standing biomass of *Mya sp.* and *Hiatella sp.* in the area and to ca. 25% of the annual production of these two bivalves. However, the macro-zoo-benthos in Young Sound includes other mollusks, crustaceans, crinoids, holothurians and polychaetes (Sejr et al. 2000) that are also eaten by walruses (Fay 1982). In August 2001, Levermann et al. (2004a) made direct observations of walrus foraging in a 1.5 km^2 study area in Young Sound (i.e. 3% of the study area in **Paper 11**). By extra-polating their estimate of predation by walruses within the observation area (i.e. 1.7 tons bivalve ww/km^2 during 90 d) to the study area (51 km^2) in **Paper 11**, the re-sulting estimate of total predation by wal-ruses during the open-water season in Young Sound is ca. 85 tons. Hence, these studies indicate that there is ample food for wal-ruses in the Young Sound study area – an area that is thought to be representative of the inshore feeding areas in East Greenland in general.

Little is known about the feeding acti-vity of walruses during winter. However, one reason that they winter in polynyas is that it gives them access to benthic food (Vibe 1950; Fay 1982). In areas such as East Greenland and the fjords of eastern Elles-mere Island and eastern Baffin Island, the fast ice prevents walruses from getting to the inshore feeding areas for a major part of the year and they are forced to stay "offshore". In East Greenland walruses occur in areas with >100 m depth during winter (**Paper 1, 6, 13**). In such areas where there is little suitable benthic food (Piepenburg 1988), they may dive to depths of at least 250 m (**Paper 13**). Walruses may survive the winter by supplementing their diet with seals and fish (e.g. polar cod) as suggested in **Paper 6**.

One might expect that walruses would lower their general activity level during winter to conserve energy. However, du-ring winter and especially during the mating season, males actively display and vocalize under water (Sjare & Stirling 1996) and likely lower their food intake at the same time as their activity level is relatively high. Walruses probably exhibit hyper-phagy during summer, or the open-water period, to replenish blubber stores. I further hypothesize that a future decrease in the extent and duration of landfast ice will

increase food availability for walruses in certain parts of their range.

Is there enough food for walruses in Greenland?

To determine the amount of food potentially available to walruses, I estimated the carrying capacity of the benthos in West Greenland and the North Water area (Table 3). The lack of good information on bathymetry prevented a similar exercise for East Greenland.

Estimates of the extent of areas with suitable walrus feeding habitat in West Greenland and the North Water area, *sensu strictu*, were obtained from unpublished sources (Greenland Institute of Natural Resources and Acquarone unpubl. data, respectively).

Data on biomass and general somatic productivity of bivalves and on mean TBM of walruses in the population were obtained from published sources (Table 3). It was assumed that walruses consume all of the soft parts of the bivalves (Fay & Lowry 1981; Fay & Stoker 1982; Kastelein et al. 1989; Kastelein & Mosterd 1989; **Paper 9**) and that they forage mainly at depths of <50 m (**Paper 9, 11**).

Theoretically, annual bivalve production in the West Greenland bank areas (<50 m deep between 66° 15′ N and 71° 30′ N) would supply the annual food requirements for ca. 10000 walruses (range: ca. 4000 to ca. 17000 animals). The estimated annual bivalve production at depths of <50 m in the North Water area may provide food for a total of ca. 15000 walruses (ca. 7000 to ca. 22000 animals) year-round (Table 3). If the areas <100 m deep are considered, those estimates can be doubled. In both areas, the respective sub-populations at their present sizes (**Paper 12**) would consume between ca. 5% and ca. 25% of the estimated annual production by the benthos.

Hence, if these estimates are in the right order of magnitude, walrus food is abundant and the numbers of walruses in the respective sub-populations are far below carrying capacity of their food resources.

Most of the foraging habitats are not available to walruses, or are not used by them, year-round. Presently, the walruses use the major mollusk banks in West Greenland only from fall to spring. In the western parts of the North Water (i.e. along Ellesmere Island) the inshore foraging banks are usually accessible during three summer months when fast ice is absent, whereas the banks on the eastern side are available for 10 months (i.e. 2 months was subtracted to account for the fact that the fast ice over the feeding areas may some-times become too thick for walruses to break through it).

Weslawski et al. (2000) estimated that walruses at Svalbard consumed between 20% and 75% of the annual bivalve production during the 16th century when they were abundant in the area. By comparison, the severely reduced present population (ca. 2000, Gjertz & Wiig 1995) consumes an estimated 1-6% of the annual bivalve production (Ibid.).

Competition for food

Other marine mammals, notably the gray whale (*Eschrichtius robustus*) and the bearded seal visit or live in the Arctic and consume benthic invertebrates as primary prey.

In contrast to the circumpolar bearded seal, gray whales no longer live in areas occupied by Atlantic walruses (Mead & Mitchell 1984). Although there appears to be some difference in their choice of floe size habitat (Simpkins et al. 2003), the range of the bearded seal broadly overlaps that of walruses and apparently the two species compete for the same trophic niche. Bearded seals are among the least selective seals with respect to haul-out substrate (they seem to prefer pack ice), provided that it overlies or is positioned near water <200 m deep. They are capable of breaking holes in solid ice <10 cm thick and they can make or at least maintain breathing holes in even thicker ice with their fore claws. During winter they concentrate in polynyas, in areas with leads and at the edges of the pack ice (e.g. Burns 2002; Kovacs 2002). However, bearded seals have a broader trophic niche than walruses. About 65% of their food consists of benthic invertebrates (as opposed to 85% in walruses) – fish and large zooplankton con-

Table 3. Sizes of potential walrus feeding grounds in West Greenland and the North Water areas, densities of walrus food, estimates of amounts of food and bivalve production in these areas, and the number of "walrus feeding year" that the benthos theoretically would be able to sustain.

Location	Foraging area < 50 m[1] km^2	Bivalve biomass density[2] (kg ww pr. m^2)	Total bivalve biomass (tons ww)	Annual somatic production[3] (tons ww)	Total bivalve biomass No. of "fye"[4]	Total bivalve somatic production No. of "fye"[4]
West Greenl.						
Average	3891	0.40	1556400	155640	101725	10173
Minimum	3891	0.15	583650	58365	38147	3815
Maximum	3891	0.65	2529150	252915	165304	16530
North Water						
Average	7600	0.30	2280000	228000	149020	14902
Minimum	7600	0.15	1140000	114000	74510	7451
Maximum	7600	0.45	3420000	342000	223529	22353

1: Estimates of areas of the West Greenland banks (0-50 and 51-100 m) between 66° 15′ and 70° 30′ outside the coastal basis-line (source: Greenland Institute of Natural Resources) were used for calculation of potential walrus food. The total bank area <100 m depth is 9754 km^2 of which 3891 km^2 is shallower than 50 m (ca. 40%). The estimate of the total area <100 m in the North Water is 19000 km^2 (Acquarone in litt. 2004). In the North Water a general lack of sounding <50 m did not allow for the establishing of a 50 m bathymetric curve. It was assumed that the ratio of area <50: <100 m was the same as in West Greenland (ca. 40%).

2: Data from literature (see text).

3: Productivity/biomass (P/B) relationship in shallow-water bivalve benthos is ca. 0.1 to ca. 0.2 (Petersen 1989; Welch et al. 1992; Brey & Gerdes 1998; Weslawski et al. 2000). A value of 0.1 (Weslawski et al. 2000) is adopted here.

4: "fye": Individual walrus "food year equivalent"=amount of bivalve/benthos wet matter needed to sustain a walrus for a year=15.3 tons/animal/year given a daily food consumption rate of 6% of TBM (**Paper 9**; Aquarone 2004) and an average TBM in the population of 0.7 tons (Fay 1982).

stitute the remainder of the diet (Pauly et al. 1998). Bearded seals consume a variety of invertebrates and vertebrates, e.g. clams, crabs, echiuroid worms, fishes (polar cod, sculpins, *Cottidae*, long rough dab, *Hippoglossoides platessoides*, and eel-blenny, *Lumpenus medius*), isopods, polychaete worms, shrimps, snails and bivalves including *Serripes*, *Astarte* and *Hiatella* (Lowry et al. 1980; Hjelset et al. 1999). According to Vibe (1950) bearded seals in Northwest Greenland never feed on clams ("mussels") and he did not think they competed with walruses for food. However, in this area bearded seals have been killed with *Serripes* remains in their stomachs (Born unpubl. data). In Northeast Greenland bearded seals reportedly live primarily on fish (mainly *Cottidae*) and only take mollusks to a limited degree (Pedersen 1942).

In the Bering and Chukchi Seas, the consumption of clams by bearded seals varied by location, year and age class. The principal species eaten in the Bering Sea was *S. groenlandicus*, of which usually only the foot was consumed (Lowry et al. 1980). At Svalbard, clams constituted only a minor fraction of the food taken by bearded seals (Hjelset et al. 1999).

The mean TBM of bearded seals is 230-250 kg (Andersen et al. 1999) whereas that of walruses is 500-900 kg (Lowry et al. 1980; Welch et al. 1992; Fay 1982) and for adult males more than 1000 kg (**Paper 4**; Fay 1982). Furthermore, walruses are highly gregarious while bearded seals are largely solitary. In contrast to bearded seals, walruses are critically dependent on shallow-water food resources (Lowry et al. 1980). When competing with bearded seals for

such resources, walruses probably have an advantage from their larger body size, tusks and gregariousness. However, I am not aware of any reports of direct confrontations between walruses and bearded seals.

In Alaska, during a period when there were signs that walruses were being affected by a decrease in their food (clam) supply, indices suggested that the population of bearded seals remained stable, perhaps owing to their more euryphagous feeding habits (Lowry et al. 1980). Similar information on numbers of bearded seals in relation to numbers of walruses is not available for Greenland. Bearded seals are widely distributed off both the west and east sides of Greenland but no estimates of abundance are available for these areas (Kapel 1992). However, the lack of good quantitative data prevents further speculation on potential competition between the two species in Greenland but my guess is that it is not really of any importance to the dynamics of the sub-populations of walruses in Greenland.

Walruses and climate

Although the paleontological evidence for the "creation of walruses" is fragmentary (**Appendix I**), some points concerning their evolution and zoogeography can be used to speculate on their ability to cope with the recent and expected future warming of the Arctic (for predictions of warming in the Arctic e.g. Hassol 2004). Modern walruses appear to have retained many traits from their ancestors, including some that enabled them to become benthic feeders in boreal and Arctic areas. However, I suggest that several of these traits may also help them adapt to future warming trends. In this section of the thesis, I review the evolution of walruses and their geographical expansion into the Arctic. The purpose is to support my hypothesis that walruses have traits from their origin further south that likely will allow them to cope with a warmer Arctic with less ice. The details of the evolution of walruses and the zoogeography of clams and walruses in Greenland that are presented in **Appendix I** are relevant for the summary here.

Time spans of the geological ages of the earth are (Jones et al. 2000):

Miocene: 23.3-5.2 Ma B.P.
Pliocene: 5.2-1.6 Ma B.P.
Pleistocene: 1.6-0.01 Ma B.P.
Holocene: ca. 10 Ka B.P. until present

The walrus – a cold water species?

Ray (1960) stated that, "unfortunately, the walrus is firmly and erroneously associated with Arctic conditions in popular thinking and in much scientific literature". Repenning et al. (1979) suggested that the modern walrus was derived from a tropical odobenid subfamily. The fossil record of walruses extends into modern temperate and subtropical latitudes, suggesting that the Arctic lifestyle of the modern species, *O. rosmarus*, is a result of recent dispersal and adaptation to boreal (Arctic) conditions (Deméré 1994a).

In the early Miocene (ca. 20-15 Ma B.P.), when thermophilic subtropical mollusks dominated in the southern Chukchi Sea (Petrov 1976), subtropical temperatures prevailed in the North Atlantic (Golikov & Scarlatto 1989). Hence, the Northern Hemisphere was not particularly cool when walruses became walruses – i.e. underwent the morphological adaptations needed feed on benthic invertebrates (cf. **Appendix I**). At 15-10 Ma B.P. a global cooling occurred with subsequent climatic oscillations (Crowley & North 1991). The mean annual temperature was ca. 4° C higher than at present in the late Miocene-early Pliocene ca. 4.3-3.3 Ma B.P. (Zubakov & Borzenkova 1988). During the Pliocene, immediately before the last glacial interval began, enormous molluskan faunas occupied the borders of the Atlantic under relatively warm conditions (Stanley 1989). In the middle Pliocene, the high sea level and temperate climate permitted a wave of Pacific mollusks to spread across the polar region and into the Atlantic. Fossils of extinct walrus genera from the late Quaternary are known from the margins of the North Atlantic and North Pacific, with *Odobenus* sp. also reported from the late Pliocene (2.7-2.0 Ma B.P.) of

the North Pacific. Other extinct odobenines lived in waters outside the Polar region, in situations known to have been warmer than in areas where they live today (*Valenictus chulavistensis* from southern California 2-3 Ma B.P.; *Trichecodon huxleyi* from Florida 4-5 Ma B.P. and Britain <2 Ma B.P.) (Fordyce 2002).

Although the Arctic Ocean was ice-covered at least seasonally, and Alaska was glaciated, perhaps 6-5 Ma B.P., Northern Hemisphere conditions were generally warmer until ca. 3 Ma B.P. (Crowley & North 1991). A significant, abrupt climate change occurred ca. 2.5 Ma B.P., initiating continental glaciation in the Northern Hemisphere and establishing the strong north-south thermal gradient characteristic of modern oceans (Crowley & North 1991; Barron & Baldauf 1989; Démére et al. 2003). Changes in the extent of sea ice and glacier ice in the Northern Hemisphere since ca. 2.5 Ma B.P. undoubtedly influenced the historical distribution of marine mammals, including walruses (Deméré et al. 2003).

During the early phases of glacial cooling, thousands of species of marine mollusks disappeared from the Atlantic Ocean and neighbouring seas. Along the Atlantic coast of North America, for example, ca. 70% of the species of marine mollusks disappeared, and the Caribbean and Mediterranean molluskan fauna was similarly decimated (Stanley & Campbell 1981; Stanley 1986, 1989). This mass reduction of mainly thermophilic mollusks – and the continued existence of cold-tolerant species – probably left little choice for walruses, which had become specialized suction feeders, but to occupy boreal waters.

During the LGM and in post-glacial time, walruses occupied areas that were not particularly cool. A walrus fossil from San Francisco (ca. 37° N) was dated to ca. 27 Ka B.P. when, judging by marine molluskan assemblages during early deglaciation, local waters probably were not much cooler than they are today (Dyke et al. 1999). It also seems quite likely that the Pleistocene *O. huxleyi* occupied a relatively "warmer" range than the recent walrus (Ray 1960; Bosscha Erdbrink & Bree 1986).

Radiocarbon dated walrus fossils from the Bay of Fundy (ca. 44° N; New Brunswick, Canada) are mainly from 10-9 Ka B.P., perhaps indicating that a large population of walruses was present there in that period (Miller 1997). Miller (1997) compared surface water temperatures in Bousfield & Thomas (1975) with occurrence of dated walrus remains and found that most walrus fossils in the Bay of Fundy dated from times when summer sea surface temperatures in the area were about 12-15° C. Furthermore, a comparison of hypothetical sea temperatures with 17th century historical records of walrus distribution indicates that walruses in the Northumberland Strait area (Fig. 3) may have inhabited waters as warm as 18° C during summer (Miller 1997). Hence, southeastern Canadian waters seem to have been occupied continuously by Atlantic walruses throughout postglacial time, even during the marine "Holocene climatic optimum", when sea surface temperatures increased sufficiently to allow entry and persistence of oysters and other thermophilic species (Dyke et al. 1999).

Historically, walruses lived in areas farther south than their present range. One interpretation, then, is that their present status as Arctic animals is due, in large part, to persecution by man (Bosscha Erdbrink & Bree 1986). In the late 1500s, Atlantic walruses lived (and reproduced) in areas farther south than their present range: Sable Island (44° N) off Nova Scotia (Allen 1880, 1930) and possibly the Orkney Islands in Scotland (59° N) (Ray 1960). During the 16th-18th centuries walruses used several *uglit* in the Gulf of St. Lawrence and Sable Island regions between ca. 44°-50° N (cf. Born et al. 1995). They numbered in the thousands on those *uglit* in April-June (Allen 1880). Walruses were extirpated from these lower-latitude areas by hunting. It is not known whether they resided there year-round or whether their distribution was continuous northward along the Labrador coast (Born et al. 1995).

Early in their evolution (cf. **Appendix I**), the walruses acquired morphological traits that are advantageous when living in icy Arctic seas: (1) Tusks that can be used to help them haul out on ice, or to chop ice, and to resist attacks by polar bears or killer

whales (*Orcinus orca*), (2) a quadruped gait for movement on ice (and land), (3) a large, rotund body to conserve energy that also facilitates breaking up through the ice, and (4) thick (2-6 cm), tough skin (Fay 1982; Brodie 2000) that, in addition to functioning as protective armor against the tusk jabs of other walruses, protects the bearer against harmful or painful contact with ice and the cold. Other morphological traits probably evolved as adaptations to life in a cold and icy environment, e.g. a thick blubber layer (up to about 10 cm; Fay 1982) and rough, highly cornified skin on palmar and plantar surfaces of the flippers that aid hauling out or walking on ice (Ibid.).

Characteristics of Northern Hemisphere shelf areas that make them suitable habitat for walruses

There are good reasons why the distribution of a specialized molluscivore like the walrus has been confined to continental shelf areas of the Northern Hemisphere. Apart from their evolutionary origin in that sector of the planet, the Northern Hemisphere has the most extensive and productive shelf areas. Arctic shelf areas, in particular, have characteristics that suit walruses and other benthic feeders.

The shallow continental shelves make up ca. 53% of the Arctic oceans. This is in sharp contrast to the rest of the world´s oceans, where the combined areas of continental shelves and slopes range between ca. 9 and ca. 18% (Jakobsson et al. 2004).

Ophiroids (brittle stars) are abundant on all Arctic continental shelves, and in fact their dominance is one of the most conspicuous features of Arctic benthic-epibenthic shelf communities (Klages et al. 2004 and references therein). However, clams and polychaetes often dominate in shelf areas with sandy or muddy sediments. In Arctic shelf areas, the typical shallow-water mollusk community is the *Macoma* community on sandy substrate in waters 3-45 m deep (Thorson 1933, 1934; Dyke et al. 1996). This community is dominated by the walrus food items *M. calcarea*, *M. truncata*,

S. groenlandicus and *H. arctica* and is fairly rich in biomass (Golikov & Scarlato 1989; Dyke et al. 1996). Furthermore, a combination of relatively greater longevity, low metabolism and generally larger size of sub-Arctic and Arctic bottom invertebrates (e.g. Petersen 1978; Sejr et al. 2002) allow for high standing biomasses and relatively high productivity, at least locally (Feder et al. 1994; Sejr et al. 2002).

Benthic communities play a much greater role in system production and turnover in shallow Arctic waters than at lower latitudes (Petersen & Curtis 1980; Grebmeier & Dunton 2000). In certain areas of the Arctic (e.g. the Bering and Chukchi Seas, Lancaster Sound, western Greenland, and the Barents Sea) marine productivity is high during summer (Nielsen 1958; Grebmeier & Barry 1991). In Arctic seas, as elsewhere, there is an inverse relationship between water depth and the relative amount of organic matter that reaches the seafloor (e.g. Berger et al. 1989; Sakshaug et al. 1994; Klages et al. 2004). In comparison with sub-tropical and tropical systems, a larger fraction of marine production settles on the seafloor in Arctic shelf areas because less production is recycled pelagically. Zoobenthic production in sub-Arctic (i.e. 69° N, West Greenland) and temperate waters (57°, N North Sea) is estimated to be 3.5-4.5 times higher than in tropical waters (8° N, Thailand) (Petersen & Curtis 1980).

A philosophical interlude or "summary" (see also **Appendix I**): Early in their evolutionary history, walruses became suction feeders on bottom invertebrates. They probably used their tusks, as do modern walruses for display and combat to establish a dominance hierarchy. Walruses evolved in ice-free temperate waters, and mating likely took place on rookeries where visual display and defense of "harems" were important. Walruses had already evolved as highly specialized feeders on bottom-dwelling benthos before the latest glaciations, ca. 2.5 Ma B.P. This cooling event exterminated a major part of the molluskan fauna at lower latitudes within the range occupied by walruses. As a consequence, walruses became confined to cooler areas in the north where cold-

resistant boreal-Arctic clams survived. Glaciation of the Northern Hemisphere forced walruses to live at the margins of the ice sheets. It was likely during this reduction in habitat that walruses adapted to boreal-Arctic conditions. Following the last deglaciation, they expanded their range northwards. The speed and timing of this expansion into various areas were determined partly by the re-colonization of bivalves, but probably more importantly by the innate characteristics of walrus behaviour and learning – in particular, their site fidelity to localized areas with predictably good conditions for wintering and foraging.

Trends in the climate of Greenland

Situated in the center of the North Atlantic Arctic, Greenland is surrounded by oceanic waters with very different physical characteristics, and Greenland's climate is influenced by major North Atlantic weather systems (Jakobsen et al. 2000; Buch 2001). Greenland has an area of 2415100 km², with a summit on the Inland Ice Cap at 3200 m altitude. The island extends from ca. 59° 47' N in the North Atlantic to 83° 42' N in the Arctic Ocean. The climate and ice conditions around Greenland are determined in a complicated and dynamic way by changes in: (a) large-scale weather systems (the North Atlantic Oscillation, NAO; the Arctic Oscillation, AO; the El Niño-Southern Ocean Oscillation, ENSO), (b) strength of occurrence and mixing of water masses of different physical characteristics and origin (East Greenland polar water, Irminger water and Sub-Atlantic water), (c) large-scale saline anomalies, and (d) local light, temperature and ice conditions (Buch 2001; Serreze et al. 2000; Hamilton et al. 2003; Liu & Curry 2004).

The three areas of walrus occurrence in Greenland (i.e. West Greenland, the northern Baffin Bay-Smith Sound region, East Greenland) differ substantially in climate and ice cover (e.g. Hansen 2001; Buch 2001). A summary of trends in temperature and ice conditions in Greenland since 1800 is given to serve as a background for eva-luation of the effects of climate on walruses in Greenland. An evaluation of the mechanisms behind these fluctuations is beyond the scope of this study.

Temperature

In historical time, walruses in Greenland have experienced long periods in which temperature conditions were both warmer and colder than at present. During the Medieval Warm Period, MWP (500-600 to ca. 1200 A.D.) annual average temperature was ca. 1° C higher than at present (Dahl-Jensen 1998; Przybylak 2003 and references therein). Among other things, this warming allowed the Norse to settle in Greenland, initiating a period of organized and possibly intensive walrus hunting at the *uglit* in the central parts of West Greenland. The Norse period in Greenland lasted until the late 1400s (Gad 1970).

The Little Ice Age (LIA) was a long, sustained cold period in the North Atlantic from 1300-1400 to 1900 (Przybylak 2003). Throughout this period, except for a few decades around 1700, the average temperature was 0.5-1.0° C colder than at present in Greenland (Dahl-Jensen et al. 1998; Przybylak 2003). The majority of temperature proxy data indicate that the greatest cooling occurred in the 19th century, earlier in Canada than in Greenland, and earlier in Greenland than in Svalbard (Ibid.).

Generally, air temperatures in Greenland decreased during the first half of the 19th century. However, since the middle of the 19th century the temperatures have increased (Dansgaard 1987; Serreze et al. 2000). The earth´s climate has warmed by approximately 0.6° C over the past 100 years, with two main periods of warming between 1910-1945 and from 1976 onwards (Walther et al. 2002). Around 1920, the Northern Hemisphere experienced a general temperature increase and temperatures remained relatively high until the 1960s (Serreze et al. 2000; Comiso 2003; Johannesen et al. 2004). The temperature increase around 1920 was seen in both western and eastern Greenland (Vibe 1967; Hansen 2001; Førland et al. 2002), Fig. 9. In West Greenland, sea surface temperatures in-

creased and remained high until ca. 1960 and then decreased (Hamilton et al. 2003). A similar trend was observed in eastern Canadian surface waters (Dunbar 1982). The climatic amelioration after 1920 markedly changed the composition of the marine fauna of western Greenland (Jensen 1939; Hansen 1949). The rise and fall of the fishery for Atlantic cod during 1950-1970 reflect the influence of this warming event on the marine ecosystem in West Greenland (Hansen 1949; Smidt 1983; Hamilton et al. 2003). Between 1950-1990 the northwestern Atlantic, including Baffin Bay and the eastern Canadian sub-Arctic region, experienced a cooling (e.g. Grumet et al. 2001).

Since 1990, mean annual air temperatures in the Northern Hemisphere – including West and East Greenland – have increased markedly (Johannesen et al. 2004), Fig. 9. Satellite thermal-IR radiometer recordings indicated that average surface temperatures were considerably warmer from August 1992 to July 2003 than from August 1981 to July 1992 in both the East Greenland-Greenland Sea area and the Baffin Bay-Davis Strait area (Comiso & Parkinson 2004). Water temperatures in the central parts of West Greenland have also

increased markedly since 1990 (Hamilton et al. 2003), Fig. 10. Annual mean air temperatures are expected to increase by 2-4° C in the Baffin Bay-Davis Strait and East Greenland areas over the period 1990-2090 (Hassol 2004).

Apparently, variation in the NAO that dates back to 1864 explains much of the inter-annual variability in weather and climate in the North Atlantic (Hurrell 1995; Hamilton et al. 2003 and references therein). Sea and air temperatures around West Greenland respond to changes in the NAO, but not in a simple, consistent way (Hamilton et al. 2003). The NAO fluctuates on a decadal time scale and may have been an important factor in climate change historically. This decadal variability in the NAO has become particularly pronounced since ca. 1950 but the causes for this shift are not clear (Hurrell 1995).

Sea ice

During the last ca. 120 years, there has been an overall decrease in the sea ice cover in the Arctic. Between 1966 and 1980, the area of the ice cover in the Atlantic sector of the Arctic has decreased by ca. 50%, and by
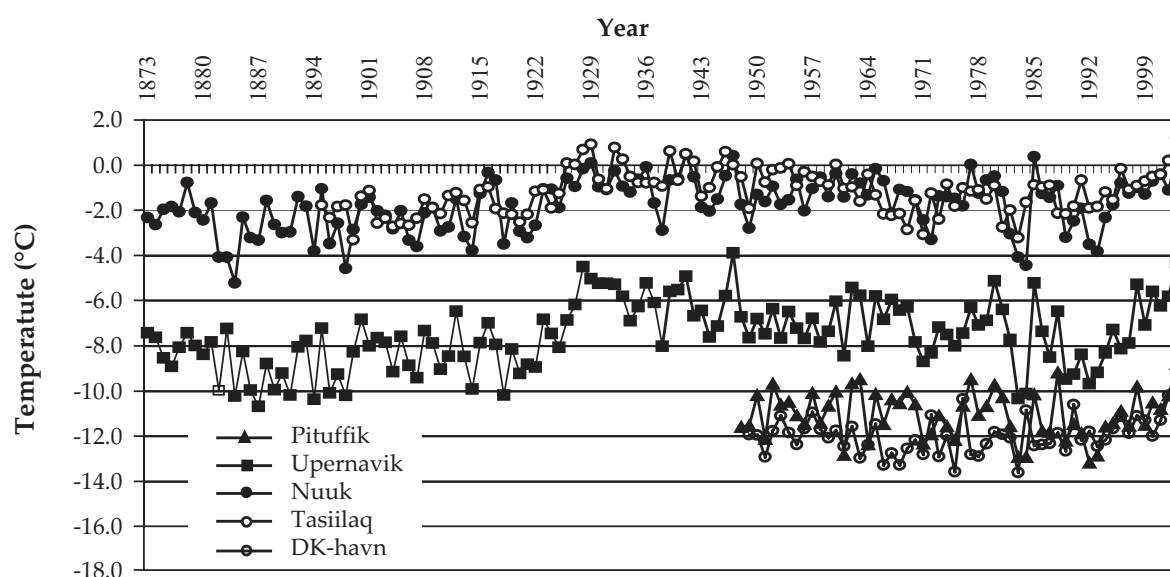

Fig. 9. Annual mean air temperatures at selected sites in Greenland, 1873-2003. The warm period during 1920s-1950s is clearly seen and so is the rapid warming since ca. 1990. Recordings were not commenced in Tasiilaq (Ammassalik, Southeast Greenland), Pituffik (Thule Air Base, Northwest Greenland) and DK-havn (Danmarkshavn, Northeast Greenland) until 1895, 1948 and 1949, respectively. Source: Danish Meteorological Institute (Copenhagen).
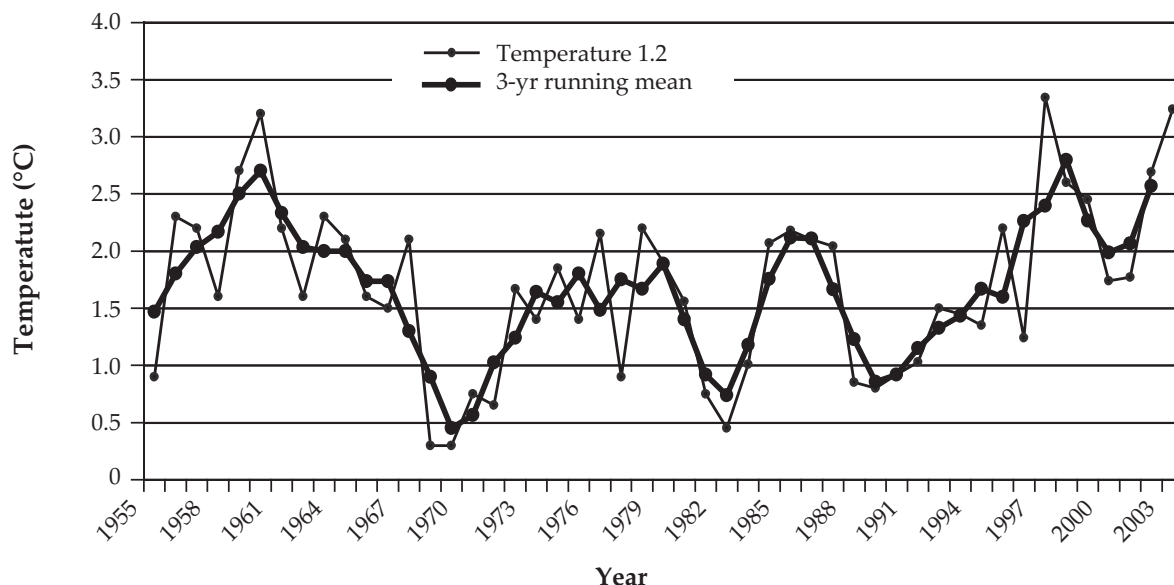
Fig. 10. Water mean temperatures in June in 0-200 depths at Fylla Bank (64° N off Nuuk in West Greenland), 1955-2004. Since 1990 there has been an increase in water temperature in West Greenland. Source: Danish Meteorological Institute and Greenland Institute of Natural Resources.

more than 50% since 1990. Ice-cover cycles, with different modes, have been noted in this region for centuries (Macdonald et al. 2004 and references therein). The extent of sea ice around Greenland has also fluctuated considerably through time (Koch 1945; Vibe 1967; Mayewski 1994; Grumet et al. 2001).

West Greenland: Except for the Storis (the "great ice" or polar ice that flows around Kap Farvel from East Greenland to Southwest Greenland), nearly all of the ice in the Davis Strait-Baffin Bay region is locally formed first-year ice (Valeur 1995). Walruses wintering in West Greenland concentrate mainly on the banks between ca. 66° 30´ and ca. 70° 30´ N (**Paper 3**). Hence, ice conditions in this area of northeastern Davis Strait are of particular importance to walruses and to those who exploit them.

To my knowledge, detailed information on ice conditions in the northeastern parts of Davis Strait prior to 1953 does not exist. However, sea ice cover is strongly linked to surface air temperature (Dunbar 1982; Comiso 2003). The "sea ice condition index" in the areas studied by Stern & Heide-Jørgensen (2003) is tightly correlated with air temperature in West Greenland (A. Rosing-Asvid, pers.comm. 2004). It there-

fore seems reasonable to assume that sea ice conditions in the northeastern parts of the Davis Strait were less severe during the period of warming (ca. 1920-1960).

In the Davis Strait-northern Labrador region, the period of ice cover increased between 1953 and 1990. No similar trend was apparent in the northern Baffin Bay-Nares Strait region (Vernal & Hillaire-Marcel 2000). Stern & Heide-Jørgensen (2003), whose study covered the eastern and central parts of Baffin Bay and Davis Strait along the coast of West Greenland, found that the amount of sea ice increased from 1953-2001. Apparently, the ice cover in northeastern Davis Strait and Disko Bay has decreased since 1993 (Ibid.).

East Greenland: Historically, the extent of the Storis along the coast of Southwest Greenland has been monitored and recorded relatively closely (Speerschneider 1931; Vibe 1967; Fabricius et al. 1995). Vibe (1967) used information on the Storis in southwestern Greenland as a proxy for the amount of ice and ice drift dynamics around the entire circumference of Greenland. He identified three major periods: (a) the "drift-ice stagnation stage" (ca. 1810-1860) when the Storis did not advance far into the Davis Strait region and

the climate of the Baffin Bay region (northern West Greenland; *sic*) was cold, (b) the "drift-ice pulsation stage" (ca. 1860-1910) when the Storis drifted into the West Greenland region in larger amounts than before, and (c) the "drift ice melting stage" (ca. 1910-1960?) when the amount of Storis decreased and temperatures increased in both West and East.

Iceland ice records also indicate more ice during the first half of the 19th century, suggesting that East Greenland also experienced cooling during this period (Vibe 1967; Grumet et al. 2000). Since ca. 1860, there has been a gradual decrease in the extent of spring sea ice off East Greenland. This decrease seems to have occurred with a decadal periodicity (Vinje 2001).

According to Vibe (1967: 22), the acceleration of drifting Storis during summer may create open water (i.e. loose ice conditions) in the Greenland Sea. In 1889, a Norwegian sealer was able to penetrate the pack ice in the Greenland Sea and reach the walrus areas of Northeast Greenland (at ca. 74° N) (**Paper 6**). Hence, this happened during a period when, according to Vibe (1967), the summer ice conditions in East Greenland may have been less dense.

The ice conditions in East Greenland reflect the fluctuation in temperature since ca. 1950. At the entrance of Scoresby Sound, the annual ice cover increased from ca. 9 months in 1953 to ca. 11 months/year in the late 1960s. Thereafter, the extent of seasonal ice cover decreased gradually to ca. 7 months/year in 1990. A similar trend was observed in the Greenland Sea (Vernal & Hillaire-Marcel 2000).

Recent and future ice conditions around Greenland: Data on sea ice concentrations received from the Scanning Multichannel Microwave Radiometer (SMMR) on the Nimbus 7 satellite and the Special Sensor Microwave/Imager (SSMI) on several defence meteorological satellites constitute the longest, quality controlled record of sea ice variability in the Arctic. This record started in 1978 (Liu & Curry 2004). Various studies demonstrate that the recent and ongoing declines in extent and thickness of ice cover in the Arctic have been greater than what would be expected from natural climate variability (Comiso 2003; Johannessen et al. 2004; Liu & Curry 2004). Longer melt periods have reduced ice volume in recent years (Comiso 2002). Thickness of Arctic sea ice varies primarily on a decadal timescale (Laxon et al. 2003).

Despite a general increase in air temperatures and decrease in summer sea ice extent in the Northern Hemisphere over the last several decades, both positive and negative anomalies have occurred simultaneously in different regions (e.g. Grumet et al. 2001; Comiso & Parkinson 2004). Regional differences in the extent of sea-ice cover (months/year) were observed in the North Atlantic Arctic between 1953-1990 (Vernal & Hillaire-Marcel 2000). A decreasing trend in the overall extent of sea ice has also been observed in the Canadian High Arctic Archipelago, Hudson Bay and the Barents and Kara Seas (Comiso 2003).

West Greenland: Various studies including different time periods and geographical areas have resulted in somewhat opposing views of the trend in sea ice cover in the Baffin Bay-Davis Strait region and adjacent areas. Sewall & Sloan (2004) modeled future sea ice development in the Arctic over approximately the next half-century, but on a very coarse scale. Their study that apparently did not include the most recent years (i.e. 2001-2004) indicated an increase in ice cover in parts of Baffin Bay. Heide-Jørgensen & Laidre (2005) studied the period 1979-2001 and found decreasing trends in amount of open water (i.e. indications of more ice) in parts of the North Water, Baffin Bay and Davis Strait regions (except at Cape Dyer on southeastern Baffin Island). However, there was very little ice at the beginning of their time series (1979 and 1980) and this could have influenced the results which could also the fact that the latest years with very little ice were not included. During 1985-2001 the area of ice in the Baffin Bay/Labrador Sea area decreased (Comiso 2003) as it did between 1978-2002 in parts of Baffin Bay and Hudson Bay (Liu & Curry 2004) and between 1978-2003 in Baffin Bay and Davis Strait (Johannessen et al. 2004). However, according to Comiso & Parkinson (2004), there was no apparent change in summer
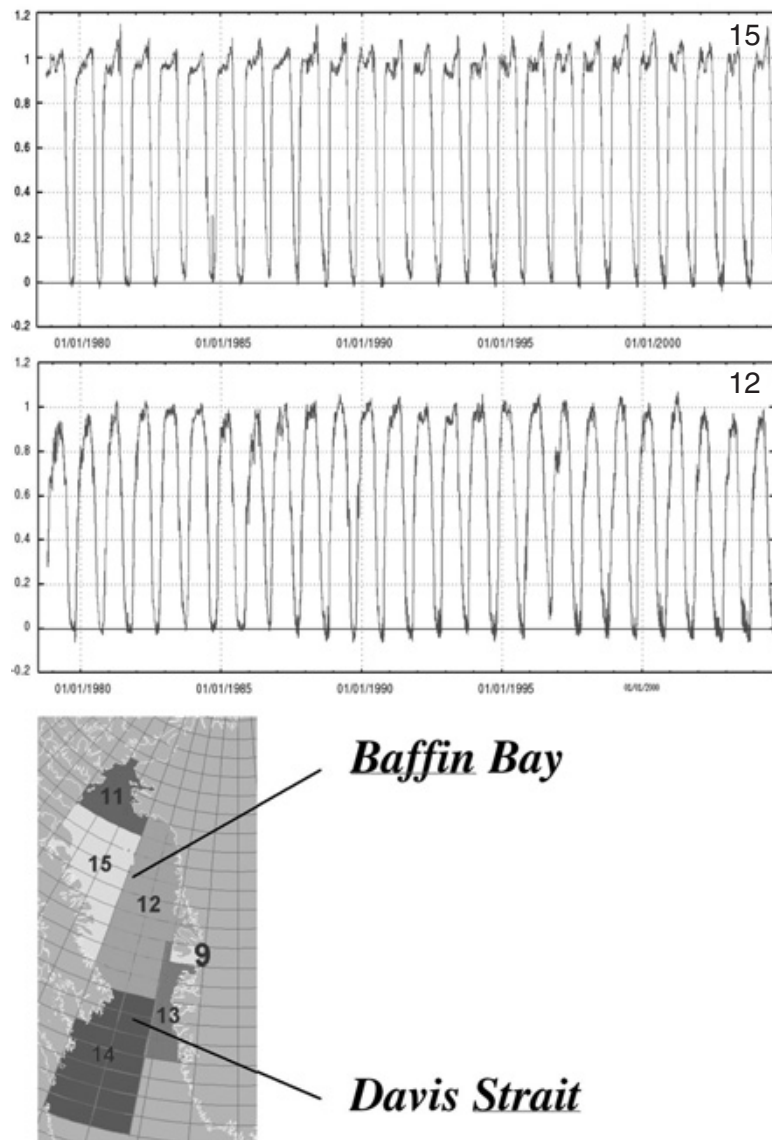
Fig. 11: Annual ice cover index for various parts of the Baffin Bay-Davis Strait area, 1979-2004 (September).

Whereas the sea ice in East Greenland has decreased during the last decades, the decrease in the Davis Strait (and eastern Baffin Bay) is more recent. West Greenland walruses winter in Area 13.

The y-axis shows annual ice cover indexed from 0 (=no ice during summer) to 1 (=winter ice cover).

Data for 1979-1987 from the NIMBUS-7 microwave-radio-meter SMMR, and for later years from the DMSP (Defense Meteorological Satellite Program) micro-wave radiometer SSM/I (number 8,11 and 13). Courtesy of: L. Toudal (Danish Center for Remote Sensing, Oersted -DTU, Technical University of Denmark).
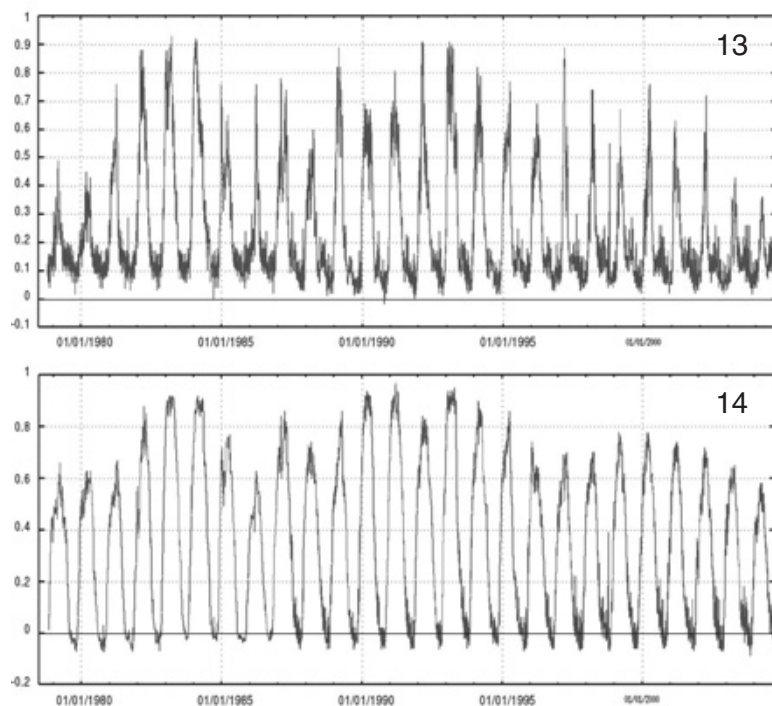
sea ice concentration in the Baffin Bay area over the 24-year period 1979-2002.

When evaluating recent trends in extent of sea ice and duration of ice cover, it may be significant that there was very little ice in northeastern Baffin Bay and Davis Strait in 2002, 2003 and 2004, Fig. 11. This paucity of ice may be within natural variation but may also reflect a trend towards less ice in those regions.

The North Water: There were no clear trends in the ice concentrations in the North Water polynya during 1980-1995 (Barber et al. 2001).

East Greenland: Generally, the sea ice cover in the Greenland Sea has become thinner during the last 2-4 decades. At the same time, the "ice-free" or "open water" period has lengthened (Maslanik et al. 1996; Rothrock et al. 1999; Parkinson 2000).

It has been predicted that by the end of the 21th century the thickness of the fast ice in inshore walrus foraging areas in Northeast Greenland will have decreased from 1.4-1.9 m to 0.8-1.3 m, and that the duration of the open-water season in these areas will have increased from 2.5 to about 5 months (Rysgaard et al. 2003a). In fact, a decrease in duration of the fast-ice period (and lengthening of the open-water period) has already been detected in East Greenland. Between 1990 and 2003, the open-water period in Young Sound increased almost linearly, from a mean of 83 d between 1990-1993 to a mean of 124 d between 2000 and 2003 (S. Rysgaard, unpubl. data).

Summary: Regardless of uncertainties associated with reconstructions of past climate and ice conditions, and notwithstanding the difficulties of predicting future trends, the overall situation in Greenland since the beginning of the 19th century can be summarized as follows: (1) It became cooler with more severe ice conditions during the first half of the 19th century, (2) temperatures increased slightly from around mid-century until ca. 1900, (3) both East and West Greenland experienced a warm period with relatively light ice conditions from the 1920s to 1960s, (4) cooling occurred from ca. 1960 to ca. 1990 in West Greenland (and East Greenland), with increased sea ice, (5) temperatures have increased markedly since 1990, resulting in a recent reduction in thickness and extent of sea ice in East Greenland and the Davis Strait region, and (6) this trend will likely continue in the foreseeable future.

A "warm" challenge to "cool" walruses

The predicted warming of the Arctic may have a negative effect on walruses (Kelly 2001; Hassol 2004). However, I offer the alternate hypothesis that walruses eventually could benefit from the warming and associated decrease in ice cover, at least in areas presently occupied by the Atlantic sub-species. Furthermore, I contend that they are morphologically and behaviorally adapted to persist in boreal conditions with little or no ice.

Based on observations of walrus distribution in the Beaufort and Chukchi Seas in 1998, Kelly (2001) suggested that the decreasing extent of summer sea ice may impede the ability of Pacific walruses to obtain food. During the summer of 1998, the sea ice in those seas retreated unusually far to the north. Consequently, substantial portions of the ice edge receded to seaward of the continental shelf – i.e. to areas where the water presumably would be too deep for walruses to forage efficiently. Without explaining the mechanistic details, Stabeno & Overland (2001) asserted that loss of a haul-out platform constitutes an immediate and clear impact on walruses from reduced sea ice in spring in the western Arctic. Also without providing details, Hassol (2004) stressed the importance of sea ice and ice edges to walruses during feeding, and he claimed that they travel long distances on floating ice, which allows them to feed over wide areas.

The tendency of walruses for preferring to haul out on ice versus land during summer is not that evident. During three seasons (August 1998-2000) when the haul-out activity of walruses was monitored on Sand Island in Young Sound in East Greenland the number of animals on land decreased when the ice concentrations (judged from photographs) reached 15-20% (Levermann et al. 2004b). However, it could

not be determined whether the walruses in such case chose to haul-out on ice instead of on land, or whether they for example left the beach because of the risk that stranded ice floes might block the escape route from the haul-out. At Bathurst Island in the Canadian High Arctic the maximum numbers on land were seen when the ice cover off the haul-out was 40-60% (Salter 1980). Likely, several factors determine whether walruses choose to haul out on land or on ice. Social mechanisms and group coherence likely play a significant role (Hills 1992; Levermann et al. 2004b).

Apparently, Derocher et al. (2004) adopted the notion that walruses rely on access to drifting ice. They hypothesized that as a result of reduced sea ice over the continental shelf, walruses (and bearded seals) could be forced offshore in search of suitable ice to use as a substrate for pupping and for resting between foraging dives. Offshore waters, however, may be too deep for walruses to forage efficiently or they may be less productive than nearshore waters. The net result would be reduced walrus (and bearded seal) abundance (Ibid.).

The scenarios described by Kelly (2001), Stabeno & Overland (2001), and Hassol (2004) may apply particularly to the situation of Pacific walruses in the Bering Strait region (see also Hills 1992: p. 92). They do not necessarily apply though to Atlantic walruses in areas where they feed inshore during summer (i.e. in eastern Greenland, the Canadian High Arctic and the Svalbard-Franz Josef Land region). On the contrary, a decrease in Arctic sea ice and consequent lengthening of the open-water period could increase the amount of time in which Atlantic walruses have access to the food-rich coastal areas. Walruses are not forced offshore by reduced ice cover but rather may spend more time inshore and thus benefit from the reduction in fast ice and the greater access to shallow-water foraging areas. Since Atlantic walruses use the inshore period to feed intensively (**Paper 11**; Levermann et al. 2004a), any prolongation of the open-water period could be expected to improve foraging conditions and enhance their populations.

Since the beginning of the 1990s, duration of the open-water season in the Young Sound study area in East Greenland (a typical High Arctic marine ecosystem) has increased markedly and may further increase by ca. 2.5 months by the end of the 21st century (Rysgaard et al. 2003a). Moreover, the frequent breaking-up of the thin ice during winter should allow walruses to feed inshore during this time of year as well as is the case in the Qaanaaq area of Northwest Greenland (Vibe 1950). Vibe (1956b) noted that walruses in this area benefited from the milder winters (i.e. in the 1940s and early 1950s) because the fast ice edge was closer to the shore and

Photo 6. During summer walruses often rest on relatively small but sturdy floes of ice. Svalbard, August 1982. *Photo: E.W. Born.*

therefore they could eat at the mollusk banks throughout the winter for a longer period of time than before. By being able to forage inshore for longer time, walruses should acquire more blubber and thus be better able to withstand, and survive, winter conditions.

During warm periods, polynyas increase in size and provide more ice-edge habitat, as indicated for the "nearshore" polynya at the entrance of Frobisher Bay, southeastern Baffin Island (Henshaw 2003). In contrast, during cold periods with severe ice conditions (and smaller polynyas), as during the Little Ice Age (LIA), ice-edge habitat is in shorter supply and "open-water" species, such as the walrus and the bearded seal, become less abundant and thus less available to human hunters (Ibid.). This reasoning suggests that it is particularly the cool periods with more and denser ice that are difficult for species like the walrus and the bearded seal that live in continental shelf areas.

Not only may walruses benefit directly from longer feeding seasons at the inshore mollusk banks, but they also may gain indirectly from increased marine productivity due to reduced ice cover. Limited sunlight and nutrient availability, low temperatures and solid ice cover are factors responsible for the relatively low productivity of Arctic waters (Klages et al. 2004). A longer open-water period would be expected to increase marine primary production (Rysgaard et al. 1999). Considering the close coupling of benthic and pelagic productivity (e.g. Sejr et al. 2000, 2002), primary and secondary production in many Arctic marine areas may increase with reduced ice cover due to global warming (Rysgaard et al. 1999). Furthermore, the benthic productivity increases with water temperature (Brey & Gerdes 1998). Improved food availability will stimulate bivalve growth and production, which could compensate for increased predation by walruses.

Based on a study in two fjords, one at Svalbard and the other at Franz Josef Land, Wlodarska-Kowalczuk & Weslawski (2001) suggested that one consequence of climate warming for Arctic marine near-shore eco-systems will be a decline in benthic bio-diversity due to increased turbidity and mineral sedimentation from melt waters. However, in Greenland, and many other areas where walruses feed near shore, the feeding banks are located at the entrance to fjords, along the outer mainland coast or farther offshore. In such areas, farther away from glaciers, turbidity caused by outflow of melt water might be less of a problem. Hence, it is possible that increased sedimentation will not negatively affect walruses to any noticeable degree.

Hassol´s (2004) statement that walruses travel long distances on floating ice may apply primarily to the situation in the Bering Strait region, where they migrate northward during spring (Fay 1982). However, although ice seems to be used as a resting place for Pacific walruses in the Bering Strait, irrespective of the direction in which the ice is moving, the principal progress in migration, however, is achieved by swimming. By swimming actively, walruses may complete their northward migration through the Bering Strait (ca. 1800 km) during spring in about a week (Ibid.). Furthermore, studies involving satellite telemetry have demonstrated that walruses travel long distances to and from foraging grounds irrespective of whether there is ice or not (**Paper 1**, **11;** Wiig et al. 1996a). This indicates that walruses take advantage of ice floes for resting when given the opportunity but also that ice as a haul-out platform is not an absolute necessity. They seem to be capable of swimming and "riding" currents to reach desirable areas even without the "passive" means of transport provided by drifting ice. However, the fact that walruses actually do haul out on ice, and perhaps in particular groups of females and young, indicates that using ice as a resting platform is of some advantage. Dispersed groups of females with calves, estimated to total more than 500 individuals were observed on small ice flows at Kvitøya, Northeastern Svalbard, in August 1987 (Gjertz & Wiig 1994). It cannot be excluded that such groups are more dependent on resting on ice floes in foraging areas than adult males. However, at this stage it seems not possible to quantify this aspect.

Walruses generally have negative buoyancy (i.e. they are heavier than sea water). However, by inflating their pharyngeal pouches (Fay 1960), they can rest in water when there is no ice (Born, pers. observation). Furthermore, in contrast to other seals, walruses can give birth and nurse in water (Fay 1982; Miller & Bonness 1983). Hence, they have adaptations that likely were acquired early in their evolutionary history when they lived in areas without ice.

Walruses often rest on ice and it is generally assumed that they depend on access to ice (Fay 1982; Manfield & St. Aubin 1991). However, in contrast to all other Arctic seals (except the more southerly distributed harbor and grey seals, *Halichoerus grypus,* that in certain parts of their range experience sub-Arctic and Arctic conditions), walruses readily haul out on land when there is little or no ice during summer. During the summers of 2002-2004, eastern Greenland had an exceptional shortage of sea ice (Toudal, Technical University of Denmark, DTU, pers. comm.; Born pers. obs.). Ice was entirely absent in the Young Sound area and offshore during late July and August when walrus studies were conducted there. The lack of ice was reflected in the number of walruses using the Sand Island haul-out. The maximum number seen on one occasion in late July and August 1998-2003 varied from year to year (1998: 28, 1999: 9, 2000: 22, 2001: 19, 2002: 19, 2003: 37; 2004: 60 (**Paper 11**; Born & Acquarone unpubl.). In 1999, when the lowest number was observed, an unusually large amount of pack ice came into Young Sound from the Greenland Sea. During 2002-2004, females with first-year calves and older calves used the haul-out, while in previous years this site was used almost exclusively used by males (**Paper 6**).

In years when the Chukchi Sea pack ice retreats seaward of the continental shelf (i.e. north of ca. 75° N), walruses have been seen to haul out on Wrangel Island in huge numbers (Fay 1982). Farther south, large numbers usually haul out on land during minimal ice conditions in September, e.g. at Little Diomede, and otherwise from May-October at several haul-outs in Bristol Bay

(Fay 1982). In the latter area, thousands of walruses (Hills 1992) routinely spend a long ice-free period in latitudes of 55-60° N where surface water temperatures are ca. 10° C during August (Fay & Ray 1968; Overland et al. 1999).

Evaluation

Following the approach of Derocher et al. (2004), who evaluated the consequences of climate change for polar bears, here I summarize the potential effects of climate change (specifically, warming and decrease in sea ice) on walruses (Table 4).

Overall, Atlantic walruses in Greenland may benefit, at both the individual and the population level, from increased productivity in near-shore waters and from greater access to inshore foraging areas. The walrus populations in Greenland can be expected to increase and expand their geographical range, leading to colonization of new terrestrial haul-outs. Such a scenario presupposes, of course, that such changes will not be offset by intensified mortality of benthos due to glacial runoff, hunting by humans or natural predators.

Increased sea temperatures may affect the composition of bivalve communities that walruses exploit. Species diversity of bivalves declines with temperature in the Pacific and Atlantic Oceans. Cold-water species generally range widely because they inhabit lower latitudes by taking advantage of cooler waters at depth (Dyke et al. 1996). Minimum winter temperatures are not critical to the distribution of mollusks, but number of consecutive days in summer when shallow-water temperatures are warm enough for spawning and larval activity is (Hall 1964; Bernard et al. 1991). Temperatures of <4° C exclude most boreal species, and only species capable of reproducing at lower temperatures inhabit Arctic waters (Thorson 1933, 1934). Cold-water mollusks tolerate a wide range of marine conditions: long winters with negative temperatures and seasonally varying salinities. They need <10° C water for reproduction and do not survive where summer temperatures exceed 20° C (optimum temperatures for reproduction of boreal species lie mostly between

Table 4. Hypothetical climate change impacts on walruses at the individual and the population level, time scale of impacts, direction and degree of projected change and potential for monitoring.

Charac-teristic	Time	Projected change	Effects				Monitoring	
			Positive	Mechanism	Negative	Mechanism	Potential	Method
Individual level								
Energy expenditure	S/M	D	++	Need of less energy for heat production	/		Good	Studies of behavior (haul-out, diving, energy expenditure)
Food consumption	S	I/D	+++	More food	+	Glacial runoff	Good	Hunting-based samples
Body condition	S/M	I	+++	More food	+	Glacial runoff	Good	Hunting-based samples
Individual growth rates	S/M	I	+++	More food	+	Glacial runoff	Good	Hunting-based samples
Calf survival	S/M	I/D	++	More food/less ice/warmer	++	More predation	Poor	Hunting-based samples (selective hunt)
Adult survival	M/L	I	++	More food/less ice/warmer	+++	More hunt	Good	Hunting-based samples
Reproductive rates	M/L	I	++	More food	/		Good	Hunting-based samples
Population level								
Food composition	L	D	/		++	Shift to food of lower quality	Good	Stomach contents analyses
Haul-out sites	M	I	+++	Increase of sites and numbers at sites	/		Good	Observations
Movement patterns/ area use	M	D/I	++	Less movement between critical habitats/more use of these	+	Over-exploitation of food locally	Fair	Tracking/surveys
Population boundaries	L	I	+++	Expansion of range	/		Good	Observations
Population size	L	I/D	+++	More food/less mortality/then decrease at K	/		Fair	Surveys
Intra-specific competition	L	I	/		++	Competition for food	Fair	Stomach contents analyses (walrus and competitors)
Inter-specific competition	M	I	/		+	Competition for food	Fair	Stomach contents analyses (walrus and competitors)
Predation/ hunting	M	I	/		+++	More hunt/ predation	Good	Monitoring of the hunts; obs. of predation at haul-outs

Time scale: S/Short =<10 yrs; M/Medium=10-20 yrs; L/Long=>20 yrs. Projected change: I=Increase; D=Decrease. Degree of effects: + = Minor; ++ = Medium; +++=Strong. K=carrying capacity; /=no entry.

5 and 15° C; Bousfield 1960). Hence, under warmer conditions, boreal bivalve species may expand their range northwards, as they did during the post-glacial warm period (**Appendix I** section "The latest expansion into the Arctic") when Atlantic walruses were present in Greenland and adjacent areas. Therefore, a general change in molluskan fauna towards more boreal species will likely not affect walruses.

Inevitably, as a population grows, the competition for food and other resources increases. This can mean that individuals increasingly consume energetically less valuable food. Fay et al. (1989) found that the body condition of Pacific walruses had deteriorated and that individuals showed signs of lowered reproductive capacity during the late 1970s and early 1980s. Also, the walruses had begun to consume lower-quality food items. Fay et al. (1989) considered those changes to indicate that the population had reached (or exceeded) the carrying capacity of its environment. However, that conclusion was not explored further in later works (Fay et al. 1997), so the question remains open as to whether the observed changes in the Pacific walrus population were indeed indicative of a density-dependent response to "over-abundance." As discussed in the section "Is there enough food for walruses in Greenland?", walruses in Greenland are probably still far below the carrying capacity of their feeding grounds.

Walruses are active predators, with tusks that allow them to kill large mammalian prey (e.g. Fay et al. 1990). In areas and seasons where the distribution of seals and walruses overlap considerably or when the walrus population is at carrying capacity (Lowry & Fay 1984), or when ice conditions make the mollusk feeding banks inaccessible to walruses, seals may well be an important food source. Therefore, walrus populations that increase and approach carrying capacity of their benthic prey do have alternative food.

Apart from humans, the main predators of walruses are polar bears and killer whales (Fay 1982; Born et al. 1995 and references therein). Polar bears prey in particular on young walruses and calves

(Fay 1982). In absence of sea ice, walruses of all age classes will be forced to use terrestrial haul-out sites more frequently, and this could expose them, and calves in particular, to increased predation from polar bears. Walrus and occasionally harbor seals are killed by polar bears when hauled out on land but according to Derocher et al. (2004) such opportunities tend to be quite local and learned by a limited number of individual bears. Although it is unlikely that predation on these species would completely compensate for the loss of opportunities to hunt ringed seals in most areas (Ibid.), one may imagine that in a situation where an increasing number of polar bears (and walruses) are forced to spend more time on land there will be an increased predation of walruses. However walruses are aware of the danger represented by polar bears and may threat the bears (Stirling 1984) and can sometimes also kill them (Freuchen 1935; Kiliaan & Stirling 1978). According to Fay (1982) "The bears probably are no match for healthy adults in direct combat".

Interactions between killer whales and walruses occur mainly during spring, summer and autumn, when the ranges of the two species overlap the most (Fay 1982). With less ice to entrap them or obstruct their movements, killer whales may be able to remain for longer periods in walrus areas, and this could result in increased walrus mortality. In general, then, mortality of walruses from predation might be expected to increase as a result of climatic warming. However, this effect would be difficult to assess quantitatively.

It is likely that the hunting pressure on walruses will increase as the amount and duration of ice cover in Arctic regions declines. The vast majority of walruses in Greenland are taken by hunters using boats (Born 1987; Born et al. 1995). If the boating season becomes longer, the catch of walruses will likely increase. A correlation between climatic amelioration and walrus catch was noted already in West Greenland, where the catch increased markedly between 1920-1940, a period when water temperatures increased and ice cover probably decreased (see sections "Catch and tempe-

rature" and "Sea ice"). With bigger boats, the hunters were able to navigate the pack ice, which had become less dense as temperatures rose. Also, walruses that have been forced to use terrestrial haul-out sites in the absence of pack ice will become easy targets if hunting is not strictly regulated, as evidenced by the disappearance of all terrestrial haul-outs in West and Northwest Greenland during the 20th century.

Finally, a reduction in ice cover will almost certainly lead to increased ship traffic and mineral development in the Arctic (Hassol 2004). Such activities are associated with underwater noise and the risk of oil spills. Underwater noise could interfere with walrus mating activity in the wintering areas and thereby reduce their reproductive efficiency (Anon. 1990a, b). Born et al. (1995) evaluated the potential effects of oil spills and concluded that because walruses are gregarious, have an affinity for shallow coastal waters, and feed primarily on benthic organisms, they are probably more vulnerable to the harmful effects of spilled oil than many other marine mammals. However, Wiig et al. (1996b) concluded that walruses probably are less vulnerable to oil exposure of the skin than thicker-coated seals. However, long-term exposure to oil and severe contamination can cause reduced survival and oil spills in feeding areas can damage or kill important prey species, and reduce the walrus food supply locally.

The possibility that climate (i.e. too warm conditions) is the principal factor limiting the southern distribution of walruses was investigated by Fay & Ray (1968) and Ray & Fay (1968) with inconclusive results (Fay 1982: 24). The average limits of thermal tolerance of adult Pacific walruses while at rest in air seem to be between -20° C and +15° C, given light winds, moderate insolation, and a cool, damp substrate on which to lie. Colder and warmer conditions may occasionally be tolerated, but only for short periods (Fay & Ray 1968). However, when the ambient temperatures become too high (or too low) walruses can retreat to the water where they can stay with a minimum production of heat (Ray & Fay 1968). Walrus herds on the beach at Round Island (58° 30' N, 160° W; i.e. same latitude as northern tip of Scotland) in June, under clear skies and in 14° C air, were as tightly packed as those on the ice in January (Fay & Ray 1968). However, under these circumstances a relatively large number of walruses also went into the water apparently in order to escape the discomfort of excessive heat (Ibid.). In Northeast Greenland walruses have been observed hauling out on the at Lille Snenæs (ca. 77° N) in 1990 in shaded air temperatures of 14.3° C and exposed temperatures of 20+° C (Born, unpubl. data). In my opinion the thermal tolerance of walrus has not been determined, and their ability to adapt physiologically to warmer conditions is not really known.

Although the aggregate effects of the factors discussed above are impossible to quantify in a meaningful way, I suggest that the positive effects of increased marine productivity and increased accessibility of walrus food will outweigh the negative effects of increased predation by polar bears and killer whales. However, the improved access of hunters to walruses, both in ice-free waters and on land, may greatly increase the risk of over-exploitation and thus negate any potential benefits to walrus populations that might come from a milder Arctic climate.

Conclusions

The present study has explored the effects of catch and climatic change on walruses. Suggested answers to the four questions posed at the outset are as follows:

(i) Exploitation by foreign and Greenlandic hunters, particularly during the 20th century, severely reduced all three sub-populations of Atlantic walruses in Greenland.

(ii) The insufficiency of information on abundance and density-dependent responses makes it impossible to reach firm conclusions on the historical effects of climatic fluctuations on the various walrus sub-populations.

(iii) Given that levels of exploitation have exceeded the intrinsic ability of walrus populations to maintain their numbers, irrespective of fluctuations in environmental carrying capacity, hunting must be seen as the main driving factor behind the dynamics (and severe reduction) of the three sub-populations of Atlantic walruses in Greenland. Warming during the first half of the 20th century resulted in a reduction in sea ice and increased the accessibility of walruses to modern hunters, leading to increased exploitation in West Greenland. A similar scenario may have developed in East Greenland. Information on ambient temperatures and catch levels is insufficient to support any conclusion concerning the North Water sub-population.

(iv) Atlantic walruses in Greenland may benefit from a warmer climate because a reduction in sea ice probably will lead to increased availability of their food. However, a future "warm" scenario in Greenland, with greater dependence of walruses on terrestrial haul-outs and increased accessibility of the animals to humans and natural predators, also could result in more intensive exploitation of walruses. Hence, expected changes in Greenland's climate over the coming years and decades give reason to reinforce and strengthen calls for strict regulation of walrus hunting.

The future

The depleted status of the West Greenland sub-population and likely also of the North Water sub-population of walruses dictates intensified studies of the effects of various hunt management scenarios. Furthermore, the effects on walruses of a warming climate and of further reduction in sea ice need to be monitored (Table 4). However, it must be emphasized that in the absence of stricter regulation of the walrus hunt in Greenland, such research and monitoring will be of only little value.

Population studies

1) The Greenland Institute of Natural Resources initiated a study in 2004 to determine the population identity and abundance of walruses wintering in West Greenland. The study, which is being conducted in cooperation with Canadian and Danish research agencies, involves the use of genetic analyses and satellite telemetry to assess the affinities between West Greenland walruses and walruses in Canada, primarily along eastern Baffin Island. Deployment of satellite tags and collection of skin biopsies for genetics are planned for 2005 in West Greenland and southeastern Baffin Island.

2) In 2004, closer monitoring of the catch of walruses was initiated in Central West Greenland between ca. 66º-ca. 72º N. This involves collection of biological samples to determine the numbers secured and the sex and age composition of the catch. Furthermore, samples of stomach contents are being collected.

3) Surveys will be conducted to estimate the numbers of walruses in the West Greenland sub-population. Survey design and areas to be sampled will be determined once the limits of the sub-population's range have been established (based on item 1).

4) Similar studies will subsequently be conducted for the North Water sub-population. Since 1999, the Department of Fisheries and Oceans (Winnipeg) have flown several aerial surveys over the summer haul-outs of the North Water sub-population in the Canadian High Arctic. The purpose was to estimate numbers. Analyses are in progress.

5) The catches of walruses reported in the "Piniarneq" since this system was introduced in 1993 are several times higher than previous estimates, in particular for West Greenland. In several instances where reports from an area appear unrealistically high, there are reasons to believe that the reports were erroneous. This calls for closer evaluation of the reliability of the "Piniarneq".

6) Although difficult to conduct, studies are needed to estimate hunting (sinking/wounding) loss rates, by area and by type of hunt.

Studies of the effects of climate change

Each summer since 1999, studies of the trophic role of walruses have been conducted at the Sand Island in Young Sound (East Greenland) (**Paper 9, 11**; Acquarone 2004; Born et al. 2004). These studies have been an integrated part of the program CAMP (Changes in Arctic Marine Productivity; e.g. Rysgaard 2003b) and part of Marin-Basis (Danish Ministry for the Environment and National Environmental Research Institute), which is intended to monitor the effects of climate change. The site is ideal for long-term studies of walruses. The response of individual walruses to changes in ice cover, food availability and climatic factors can be monitored, as can the group's response to annual fluctuations in ice cover and climate.

1) Studies in 2002-2003 involved determination of the numbers of animals in the group using the haul-out, and assessing site fidelity. All walruses using

the haul-out in 2002 and 2003 were identified individually from microsatellites (nuclear DNA markers) extracted from skin biopsies. These "marks" were used to estimate the numbers of individuals using the Sand Island haul-out (Born & Andersen unpublished data). It is planned to repeat the sampling in the future to assess trends in abundance, which in turn can be correlated to trends in ice cover. Also, further information on longevity, growth and long-term site-fidelity will come from a repeated study at this site.

2) In August 2004, fat biopsies were collected from the walruses on the Sand Island. At the same time, selected walrus food items were sampled from the sea-floor nearby. Satellite tags were put on 4 individuals to determine the locations of feeding areas. The purpose of the study is to use fatty acids to determine composition of the food eaten by walruses. This study is to be repeated in the future to assess changes in food preferences, which might in turn reflect changes in climate and/or intraspecific competition. A comparison of fatty acids in walrus fat samples from Svalbard (Norwegian Polar Institute), Northwest Greenland (National Environmental Research Institute) and West Greenland will allow an assessment of regional differences in diet.

3) Each year, information is collected on the numbers of walruses that haul out on Sand Island as well as on dates of first arrival and departure. The purpose is to study trends in use of the haul-out and in length of the inshore occupancy period, again possibly reflecting variation in ice cover.

4) Mapping the locations of all (past and present-day) terrestrial haul-out sites throughout the range of the Atlantic walrus would be useful in efforts to detect range expansion (or shrinkage) and trends in numbers.

5) In Greenland, where walruses are hunted by Greenlanders, samples should be collected from killed animals and used to estimate vital parameters (e.g. age at first reproduction). If such samples were also obtained from for example Foxe Basin in Canada and from Northwest Greenland, new estimates of reproductive parameters could be compared with previous estimates. Furthermore, samples from the catch can be used to detect changes in blubber thickness (response to food availability) and fatty acid composition.

Regulation of the hunt

In Greenland, walrus hunting is regulated according to laws issued by the Greenland Home Rule Government. The latest regulations (Anon. 1998) allow walruses to be hunted only by persons with a Greenlandic hunting license. Between 1 May and 28 February, taking walruses is prohibited between 66° N and 70° 30′ N. North of 70° 30′ N in West Greenland, and in East Greenland outside the "National Park of North and Northeast Greenland", walruses can be taken year-round. In West Greenland south of 66° N, walrus hunting is prohibited year-round. Only vessels weighing less than 20 tons (BRT) and dog sleds can be used for hunting walruses. There are restrictions concerning the types of weapons and bullet types that can be used. It is stated explicitly that wounded walruses must be harpooned before being killed and that all hunting products must be brought back or cached. It is mandatory that hunters report their catches (number, sex, age, date etc.).

No catch quotas exist for any of the walrus sub-populations in Greenland, despite the fact that catches from the West Greenland sub-population, and apparently also from the North Water sub-population, have been unsustainable for many years if not for decades. Furthermore, walruses may, because of ongoing trends in climate and ice cover, become more accessible to hunters using motorized vessels. In situations with less severe ice conditions, walrus habitat becomes easier to navigate and search in a short time. Also, as walruses become increasingly dependent on terrestrial haul-outs during summer, they become an easier target for hunters. Hence, exploitation of walruses in a warmer Greenland will require strict regulation – as witnessed by the disheartening history of the walrus in West Greenland during the first half of the 20th century.

Acknowledgments

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This list does not include the papers that are a part of the thesis – see "List of Papers".

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Appendix I

This appendix summarizes the evolution of walruses and their early expansion into the boreal and Arctic areas, including their immigration to Greenland. It also reviews the development of Arctic shelf areas, the link between walruses and bivalves in Greenland. The purpose is to provide a background for understanding the niche of walruses in the Arctic and not at least in the Greenlandic marine ecosystem.

Time spans of the geological ages of the earth are (Jones et al. 2000):

Miocene: 23.3-5.2 Ma B.P.
Pliocene: 5.2-1.6 Ma B.P.
Pleistocene: 1.6-0.01 Ma. B.P.
Holocene: 10 Ka B.P. until present

Where did walruses come from?

The evolution and zoogeography of walrus-like pinnipeds and of walruses have been reviewed and discussed by, among others, Repenning & Tedford (1977), Deméré (1994), Kohno et al. (1995) and Deméré et al. (2003).

Morphological data based on fossils indicate that odobenids have a common origin with otariids in the North Pacific Ocean, dating to the Miocene sometime before 18 Ma B.P. (Repenning & Tedford 1977; Deméré et al. 2003). Fossil walruses are known only from the Northern Hemisphere (an exception is an unconfirmed walrus skull from the Miocene or Pliocene of coastal Peru) (Deméré 1994). The oldest records of odobenids are from the North Pacific from the late early Miocene (Deméré 1994; Deméré et al. 2003). Odobenids diversified and flourished 10-8 Ma B.P., with the more modern forms dispersing from the North Pacific into the North Atlantic by the early Pliocene (5-4 Ma B.P.)(Deméré et al. 2003). Late Miocene fossils have been found in the western United States, Mexico and Japan (Deméré 1994). Pliocene walruses are known from the eastern and western United States, Great Britain, Belgium and Japan, and Pleistocene walruses have been recorded from the eastern and western United States, Canada, Great Britain, the Netherlands, France and Japan (Ibid.).

The historical biogeography of the modern genus *Odobenus* is difficult to determine because of the limited nature of the fossil record (Deméré et al. 2003). It has been hypothesised that the tusked walruses originated in the North Atlantic in the late Miocene and that the genus *Odobenus* evolved in that ocean basin. According to this hypothesis, the sub-tropical or tropical *Aivukus*-like non-tusked walrus spread from the North Pacific into the North Atlantic through the Central American Seaway 8-5 Ma B.P., and odobenids then became extinct in the North Pacific during the Pliocene, some 5.3-1.6 Ma B.P. (Repenning et al. 1979). After having adapted to Arctic conditions in the North Atlantic, the modern tusked walruses (*Odobenus*) entered the North Pacific via the Arctic Ocean during the late Pleistocene, some 600 Ka B.P. (Repenning & Tedford 1977; Repenning et al. 1979). However, finds of odobenid fossils in the western North Pacific (Tomida 1989; Miyazaki et al. 1992) and the succession of occurrence of tusked odobenids in the North Pacific from the late Miocene to the Recent suggest that odobenids might have evolved there during the late Miocene and thus never disappeared from the North Pacific (Kohno et al. 1995; Deméré et al. 2003). According to Kohno et al. (1995), the genus *Odobenus* probably evolved in the North Pacific and dispersed into the Arctic Ocean and then to the North Atlantic during one of the early interglacial events of the late Pliocene or Pleistocene.

The subfamily Odobeninae has been defined as a monophyletic group containing *Odobenus* together with the extinct *Valenictus*, *Aivukus*, *Protodobenus*, *Pliopedia*, *Prorosmarus* and *Alachterium*, with uncertainty about the phylogenetic positions of the last 5 of those genera (Deméré *et al.* 2003).

Other odobenine walruses (*Alachterium*, *Valenictus*) likely became extinct sometime in the mid-Pliocene around 2.5 Ma B.P. (Anon. 2002b), i.e. at the beginning of the last Ice Ages.

The archaic walruses (*Neotherium* and *Imagotherium* of the mid to late Miocene) had un-enlarged canines and narrow, multiple, rooted premolars, adaptations that suggest they retained a fish diet, as hypothesized for other archaic pinnipeds (Berta 2002). A pronounced feature of *Odobenus* is paired tusks (i.e. elongated upper canines) found in adults of both sexes (Deméré 1994). Tusks evolved independently in the Odobeninae and Dusignathinae (the latter "crown clade" remained endemic to the North Pacific region until extinction 3-2 Ma B.P.; Deméré et al. 2003; Fordyce 2002). However, dusignathines had enlarged lower as well as upper canines (Deméré 1994).

The enlargements of the upper canines in the tribe Odobenini (new taxon, Deméré 1994) and the associated development of a central globular dentine column, first evolved in the most recent common ancestor of *Alachtherium*, *Valenictus*, and *Odobenus*, comprise strong evidence that the tusks of the modern genus *Odobenus* were inherited. Hence, tusks do not represent adaptations to the present Arctic and sub-Arctic range of *Odobenus*; rather, they are structures that were already present and functional when the temperate or subtropical ancestors of *Odobenus* arrived in boreal regions (Deméré 1994).

When walruses became walruses

The most prominent feature of modern walruses may be their tusks, but it was also important for the animals to have acquired their specialized suction-feeding method for eating clams. It was only after developing that capability that they could be considered "real" walruses in an ecological (i.e. non-paleontological) sense. The specialized suction-feeding strategy evolved secondarily in odobenine walruses and their sister group Dusignathinae. The shift away from pelagic-piscivory to benthic-mollus-civory occurred during the Miocene – at least 11 Ma B.P. (Berta & Sumich 1999). The morphological changes associated with adaptation to suction feeding in odobenine walruses created higher negative pressure in the oral cavity. These changes were: arched palate, fused lower jaws and robust cranial symphysis. At the same time, the incisors became reduced (Berta & Sumich 1999). Fay (1982) suggested that this change in feeding capability and strategy enabled the positive pressures of social advantage to prevail and allowed the upper canines to evolve into tusks.

Early geographical expansion

With the onset of cooling and glaciation in the late Oligocene, the oceans became thermally stratified, with cold bottom water, strong surface circulation gyres and long-range thermohaline circulation. These physical changes, and the development of extensive areas of coastal upwelling, enhanced the productivity of high-latitude ocean regions (Fordyce 1980). The increased productivity, together with the opening and closing of seaways, glacial and interglacial climatic events and changes in ocean circulation patterns, played a major role in the radiation of marine mammals (Deméré et al. 2003).

The opening of Bering Strait about 5.5-4.8 Ma B.P. (i.e. late Miocene-early Pliocene), with waters flowing through the strait from north to south, facilitated the dispersal of Arctic and North Atlantic mollusks into the North Pacific. Associated with the closure of the Central American Seaway, the flow of surface water through Bering Strait changed direction ca. 3.5 Ma B.P. (i.e. in the mid Pliocene). The resulting south-to-north flow established the modern Arctic Ocean circulation pattern and facilitated the dispersal of Pacific mollusks into the Arctic and the North Atlantic as far as the European coast (Símonarson et al. 1998; Marincovich 2000). Although there is no direct fossil evidence, walruses could have participated in these faunal interchanges (Deméré et al. 2003).

Closing and opening of Bering Strait during the late Pliocene and Pleistocene periodically isolated the North Pacific from the Arctic Ocean and the North Atlantic (Deméré et al. 2003). It has been suggested that the Pacific and Atlantic walrus sub-species diverged during the late Pleistocene due to glacial and sea ice barriers in the Arctic (Davies 1958; Dyke & Prest 1986). Davies (1958) suggested on morphological grounds that the separation between the *divergens* and *rosmarus* sub-species dated from a glaciation earlier than the last, and that effective mingling of the two populations had not taken place since then. A phylogenetic analysis of mtDNA showed that Atlantic and Pacific walrus haplotypes represent separate monophyletic groups and mtDNA sequence divergence between haplotypes suggested separation of the sub-species about 500000 to 785000 years ago (Cronin et al. 1994).

The latest expansion into the Arctic

During the Pleistocene, climatic fluctuations that had begun in Pliocene continued. The last glacial period (the Wisconsinan or Würm Ice Age) lasted from 125-120 to ca. 15-10 Ka B.P. (Létreguilly et al. 1991; Dansgaard et al. 1993).

Most of the Atlantic walrus's historical range was covered by glacial and sea ice at the Last Glacial Maximum (LGM) about 20-21 Ka B.P. (Frenzel et al. 1992; Dyke et al. 1999; Vernal & Hillaire-Marcel 2000; Vernal et al. 2000). Consequently, the animals must have been displaced far to the south at that time (Dyke et al. 1999). The vast extension of the ice sheet into the Atlantic at the LGM (Hughes et al. 1981) probably forced walruses south to ca. 40° N in North America (i.e. close to the New York area) and to ca. 50° N in the vicinity of the English Channel in western Europe. Hence, their distribution reached much farther south than implied by late Pleistocene occurrences of *O. rosmarus* (Bree & Bosscha Erdbrink 1990; Bosscha Erdbrink & Bree 1999).

The oldest Pleistocene walrus fossil (the "Qualicum walrus"), found in glaciomarine

sediments on Vancouver Island, is perhaps nearly 70000 years old (Harington & Beard 1992). Another fossil found in San Francisco harbor is probably ca. 27000 years old (Dyke et al. 1999). All other radiocarbon-dated North American walrus fossils are from the Atlantic and are of late-glacial or postglacial age (Ibid.). Finds of 24000-31000-year-old walrus fossils in the North Sea and Denmark indicate that walruses were a "Danish" faunal element during the last ice age (Møhl 1985). A huge ice sheet covered Scandinavia then (e.g. Hughes et al. 1981), and the walruses probably lived close to its margin. In those areas of the North Atlantic where walruses lived during glacial maxima there are no vast continental shelves. This reduction in range in suitable habitat, and likely also in abundance in the western and eastern Atlantic probably had a "bottle-neck" effect that could explain the genetic differences between walruses to the west and to the east of Greenland found by Andersen et al. (1998) and in **Paper 8**.

The record of the walrus's northward expansion after the LGM in the Canadian Arctic is emerging as more fossils found and described on the American continental shelf, in the Gulf of St. Lawrence and Bay of Fundy, and along the southern coast of Labrador (Dyke et al. 1999). The oldest radiocarbon-dated walrus fossils from eastern North America between 41.5 and 51.5° N (i.e. New York to Newfoundland) are ca. 13.0-11.5 Ka B.P. old. In contrast, the oldest fossils found between ca. 70° and 78.9° N in the Canadian Arctic are ca. 9500 to ca. 10000 years old (Dyke et al. 1999: fig. 7). Judging from the fossil evidence, the Atlantic walrus evidently began invading the newly de-glaciated coastal areas of North America by moving northward from its LGM "refugium" at the earliest opportunity. Its northern limit advanced from the vicinity of the glacial limit (i.e. around New York), reaching the Bay of Fundy by 12.7 Ka B.P., the Grand Banks by 12.5 Ka B.P., southern Labrador by 11.5 Ka B.P. and the Canadian Arctic Archipelago by 9.7 Ka B.P. Remains dating from 9.7 Ka to 8.5 Ka B.P. and from 5.0 to 3-4 Ka B.P. are the most common (similar to what is true for the bowhead whale *Balaena mysticetus*), suggesting that

fluctuations in environmental conditions, probably driven by climatic events, exerted a strong influence on walrus distribution and abundance (Dyke et al. 1999). Hence, walruses may have dispersed into new areas and expanded their range (and numbers) during periods with a comparatively warm climate.

Most of the present coastal range of walruses in Greenland as well as the most of the Greenland continental shelf was covered by glacial ice during the LGM and early deglaciation (Meinert et al. 1992; Dyke et al. 1996; Funder & Hansen 1996; Gordillo & Aitken 2000; Bennike & Björck 2002). However, the North Greenland shelf experienced only limited glaciation during the LGM (Funder & Hansen 1996).

Radiocarbon-dated mollusk shells from Central West Greenland indicate that the shelf and outer coastal areas had become de-glaciated and flooded by 13-12 Ka B.P., and those in Northwest Greenland by ca. 10 Ka B.P. (Kelly 1985). However, in the central areas of East Greenland (i.e. Scoresby Sound and north), the de-glaciation may have started already by 15 Ka B.P. (Funder & Hansen 1996). By about 10-8 Ka B.P. the glaciers in Greenland had melted sufficiently that nearly all of the walrus's present near-shore habitat had become ice-free (Funder 1989a,b; Dyke et al. 1996; Gordillo & Aitken 2000).

Foraminiferan assemblages indicate that the oceanic polar front was located far south in the North Atlantic during the period 20-13 Ka B.P. At about 13 Ka B.P. the front abruptly retreated northwestwards, and warmer surface waters entered the northeastern North Atlantic (Jansen et al. 1983). After a cooling during 11-10 Ka B.P. that brought the polar front and the summer sea ice limit farther south in the Northeast Atlantic, ocean temperatures rose again (Ibid.; Koc et al. 1993). Diatom-based paleoceanography indicates that during 19-15 Ka B.P. the polar front lay along western Norway, where there was open water. Due to an influx of warm Atlantic water between 11-9 Ka B.P., the Arctic sea ice receded rapidly, reaching a minimum extent 9 Ka B.P. (Miller et al. 2001). At this time the coasts of Norway and Svalbard were ice-free whereas sea ice covered the Northeast

Greenland coast north of Scoresby Sound (Ibid.). Hence, after the LGM walruses may have dispersed northwards from Norway to Svalbard during post-glacial times and managed to reach East Greenland from the Svalbard area after 9 Ka B.P.

During the "warm period" or "climatic optimum" in the Holocene ca. 8 to ca. 5-4 Ka B.P., when average temperatures were 2-4° C warmer than at present (Johnsen et al. 1995; Dahl-Jensen et al. 1998), the Greenland Inland Ice Cap was less extensive than it is now (Weidick et al. 1990; Weidick 1996). The waters of the Canadian Arctic, the Baffin Bay region and Greenland experienced a corresponding warming around that time (Funder & Fredskild 1989; Williams 1990; Dyke et al. 1996; Gajewski et al. 1999).

Although Dyke et al. (1999) were able to list a total of 59 radiocarbon-dated walrus fossils from southeastern Canada and the Canadian Arctic archipelago, walrus fossils from Greenland are remarkably scarce – and more recent than those found in Canada (Weidick 1992; Bennike 1997). Four finds (5.5-2.6 Ka B.P.) have been made in West Greenland between 62° 30' N and 70° 10 N (Weidick 1992; Bennike 1997; Nelson & Takahashi 2004; E. Rosing pers. comm. 2004) and 2 finds (1.9-1.5 Ka B.P) have been made in Peary Land in Northeast Greenland (ca. 82° N). The locations of the two oldest Greenland specimens at Ilulissat/Jakobshavn and Aasiaat/Egedesminde, respectively, indicate that walruses lived in the region at a time when the Inland Ice margin was east of its present position (Bennike 1997).

Although one must be cautious when interpreting the biogeographical significance of the few walrus fossils from Greenland, the scantiness of the material and its young age in comparison with that in Canada lead me to suggest that walruses immigrated to Greenland fairly recently - perhaps towards the end of the post-glacial warm period. Immigration would have been delayed despite the fact that invertebrate walrus food items, including bivalves, were present in Greenland soon after the de-glaciation (Funder & Fredskild 1989; Funder & Hansen 1996; Bennike 1997; Bennike & Björck 2002).

In summary, walruses apparently colo-

nized the Canadian Arctic relatively rapidly during de-glaciation, whereas they arrived in Greenland relatively late. In this connection, it is worth noting that the earliest Greenland fossils of marine mammals – ringed seals and bowhead whales (*Balaena mysticetus*) – are from 9.0-8.5 Ka B.P. (Bennike 1997). The Holarctic ringed seal is omnivorous (e.g. Helle 1992) whereas the disjunctly distributed bowhead whale consumes pelagic crustaceans (e.g. Lowry 1993). These mobile species that feed on pelagical and seasonally available prey were probably able to expand their post-glacial range into Greenlandic waters earlier than the largely stenophagous and highly site-tenacious walrus.

The colonization of West Greenland by walruses probably happened during the "Holocene climatic optimum" when boreal mollusk species extended their range northwards in Canada and in East and West Greenland (Andrews 1972; Hjort & Funder 1974; Funder & Weidick 1991; Dyke et al. 1996). Although marine conditions apparently lagged somewhat behind the terrestrial climate change (Andrews 1972), there was a marked reduction in pack ice during this thermal maximum (Davies 1958). In addition, eustatically conditioned transgression in East Greenland may have taken place 6 Ka B.P., and in West Greenland sea level may have been more than 20 m higher than at present some 4.5 Ka B.P. (Funder 1989c). Hence, a combination of warming with less pack ice and the greater area of shallow-water foraging habitat may have facilitated the immigration of walruses to Greenland ca. 5 Ka B.P.

The relatively late immigration of walruses into Greenland after the LGM, and their poor ability to re-colonize previously occupied ranges with suitable food, might be explained by the same factors: their stenophagous foraging habit and dependence on areas with suitable mollusk banks, in combination with their social organization (i.e. gregariousness). Immigration of walruses to West and East Greenland was probably impeded by the fact that they first had to move through areas that were (and still are) uninteresting from a walrus point of view. To reach West Greenland from

Canada via Northwest Greenland they would have had to cross Melville Bay, where there is only little suitable walrus habitat, and to reach it more directly from the west or east, they would have needed to cross the deep waters of Davis-Strait-Baffin Bay or the Greenland Sea-Fram Strait (ca. 400 km in either case).

Development of Arctic shelf areas and the link between walruses and clams

Walruses are "linked" to shelf areas with bivalve food. Hence, the development of these areas in the Northern Hemisphere and their bivalve fauna are summarized here because they are of basic importance to the distribution of present-day walruses.

Important aspects of present-day mollusk distribution in the Arctic were influenced by several factors: stresses of Quaternary temperature fluctuations, segregation of North Pacific and North Atlantic ranges during glaciations, and extensions and retractions of ranges in connection with glaciations (Lubinski 1980). Only very adaptive species survived the changes associated with the early Quaternary glaciations, which explains the lack of extinctions during the last glaciation, i.e. those that were ill-adapted had already been purged in previous glaciation episodes (Dyke et al. 1996).

About 2.5 Ma B.P., the Arctic Ocean was inhabited by a benthic fauna of mainly Pacific origin that was brought through the Bering Strait by the closure of the Central American Seaway (Símonarson et al. 1998; Marincovich 2000). Boreal conditions prevailed at that time in the ice-free Artic Ocean, where Atlanto-boreal species of Mediterranean-Lusitanian origin were also found (Strauch 1972; Golikov & Scarlato 1989).

The Arctic Ocean and Greenland Sea may have been relatively warm during the early glaciations of Northeast Greenland (2.4-2.6 Ma B.P.) (Penney 1993) or, alternatively, they may have returned to warm conditions ca. 2.0-1.8 Ma B.P. (Bennike & Böcher 1990). However, associated with the subsequent cooling, boreal species of the Arctic Ocean and the continental shelves of

the Arctic could not cope with the harsh environment and eventually became extinct. During the first glaciation, only deep-water mollusks were able to survive, and only at the ice margins (Golikov & Scarlato 1989; Símonarson et al. 1998).

About 400-350 Ka B.P., temperatures rose and ice sheets melted, resulting in dispersal of marine fauna on the shelves and wider distribution of the estuarine Arctic fauna. Temperatures rose to 3-4° C in the Arctic Ocean (Golikov & Scarlato 1989). Then, 240-250 Ka P.B., severe cooling commenced (Dansgaard et al. 1993). Despite the very cold conditions, some species survived – the same species that inhabit the Arctic today. The first shelf fauna to appear after the melting of the last ice sheet consisted of the estuarine-Arctic assemblages that had survived the glaciation in the eastern sector of the Arctic.

During the Holocene (i.e. the last ca. 10000 years), temperatures have varied markedly (Przybylak 2003). They rose by 2-3° C from 6-4.5 Ka B.P. During this period, subtropical and boreal species extended their range northward. In the Canadian Arctic this "Holocene climatic optimum" lasted from 10-8.3 to 4.5-3.0 Ka B.P. In the Svalbard area there was a post-glacial "warm period" between 7-4 Ka B.P. (Przybylak 2003).

Another important feature of Pleistocene geography was the rise and decline of sea level resulting from the alternating capture and release of water by ice sheets (Davies 1958; Fairbanks 1989; Golikov & Scarlato 1989; Tushingham & Peltier 1991; Przybylak 2003). In the early phases of de-glaciation following the last ice age, eustatic sea level was 50-75 m lower than at present (Fairbanks 1989; Przybylak 2003) but the sea level raised relatively soon after. The sea level elevation increased from ca. 40 m below present at ca. 12 Ka B.P. to ca. 10 m below present around 9.5 Ka B.P. It then increased more or less gradually to the present level (Przybylak 2003; Tushingham & Peltier 1991). About 6 Ka B.P. the oceans attained their present levels, and 5-4.5 Ka B.P. the levels were 2.5 m higher than today (Goli-kov & Scarlato 1989). These sea-level variations resulted in alternating depopulation and recolonization of vast sub-littoral habitats and influenced the diversity of marine benthic communities as well as the adaptability of benthic organisms (Klages 2004). In turn, these processes almost certainly would have influenced the distribution of walruses.

Papers

Paper 1
Born, E.W. & L.Ø. Knutsen 1992.
Satellite-linked radio tracking of Atlantic walruses (*Odobenus rosmarus rosmarus*) in northeastern Greenland, 1989-1991. *Zeitschri für Säugetierkunde* 57: 275-287.

Paper 2
Born, E.W. & I. Gjertz 1993
A link between walruses (*Odobenus rosmarus*) in northeast Greenland and Svalbard. *Polar Record* 29 (171): 329.

Paper 3
Born, E.W., M.P. Heide-Jørgensen & R.A. Davis 1994
The Atlantic walrus (*Odobenus rosmarus rosmarus*) in West Greenland. *Meddelelser om Grønland, Bioscience* 40: 1-33 pp.

Paper 4
Knutsen, L.Ø. & E.W. Born 1994
Body growth in Atlantic walruses (*Odobenus rosmarus rosmarus*) from Greenland. *Journal of Zoology (London)* 234: 371-385.

Paper 5
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Haul-out activity of male Atlantic walruses (*Odobenus rosmarus rosmarus*) in northeastern Greenland. *Journal of Zoology (London)* 243: 381-396.

Paper 6
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. *Meddelelser om Grønland, Bioscience* 46:1-73.

Paper 7
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Reproduction in female Atlantic walruses (*Odobenus rosmarus rosmarus*) from northwestern Greenland. *Journal of Zoology (London)* 255:165-174.

Paper 8
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A review of the genetic relationships of Atlantic walruses (*Odobenus rosmarus rosmarus*) east and west of Greenland. *Polar Biology* 24 (10): 713-718.

Paper 9
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Paper 10
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Reproduction in male Atlantic walruses *(Odobenus rosmarus rosmarus)* from the North Water (N Baffin Bay). *Marine Mammal Science* 19(4): 819-831.

Paper 11
Born E.W. & M. Acquarone 2005
An estimation of walrus predation on bivalves in the Young Sound area (NE Greenland). *In:* S. Rysgaard & Glud, R.N. (eds.) Carbon cycling in Arctic marine ecosystems. Case study – Young Sound. *Meddelelser om Grønland Bioscience.* In press

Paper 12
Wiing, L. & E.W. Born 2005.
An assessment of Greenland walrus populations. *ICES Journal of Marine Science* 62: 266-284.

Paper 13
Born, E.W., M. Acquarone, L.Ø. Knutsen & L. Toudal 2005
Homing Behaviour in an Atlantic Walrus (*Odobenus rosmarus rosmarus*). *Aquatic Mammals* 31(1): 11-21.

An assessment of the effects of hunting and climate on walruses in Greenland

By

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