*Working paper to the NAMMCO workshop on walruses in the North Atlantic,*
*Copenhagen, 11-14 January 2005.*

# POTENTIAL EFFECTS ON ATLANTIC WALRUS OF WARMING IN THE ARCTIC

**E.W. Born[1] & Ø. Wiig[2]**

1) Greenland Institute of Natural Resources, P.O. Box 570, DK-3900 Nuuk, Greenland
2) Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, NO-0318 Oslo, Norway.

## Introduction

It has been suggested that the predicted warming of the Arctic may have a negative effect on walruses (Kelly 2001; Stabeno & Overland 2001; Hassol 2004; Derocher et al. 2004). I this working paper we offer the alternate hypothesis that walruses eventually could benefit from Arctic warming and associated decrease in ice cover. We contend that walruses are morphologically and behaviorally adapted to persist in boreal conditions with little or no ice. Although walruses in general are considered, we concentrate on the situation of the Atlantic subspecies (*Odobenus rosmarus rosmarus*).

## The walrus: a cold water species?

Although the paleontological evidence for the “creation of walruses” is fragmentary, 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.

Early in their evolution, the walruses evolved morphological traits that were advantageous later 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 (*Ursus maritimus*) 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 smashing through ice; and (4) thick (2-6 cm), tough skin 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 (Fay 1982; Brodie 2000). Other morphological traits probably evolved later 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.).

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).

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). 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 sense. The shift to molluscivory happenede at least 11 Ma B.P. (i.e. million years before present) (Berta & Sumich 1999).

The northern hemisphere was not particularly cool when walruses became walruses - i.e. underwent the morphological adaptations needed feed on benthic invertebrates. The mean annual temperature was ca. 4 ºC 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). 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 walruses live today (Fordyce 2002).

During the Last Glacial Maximum and in post-glacial time, walruses occupied areas that were not particularly cool. A walrus fossil from San Francisco (ca. 37º N) was dated to ca. 27 Ka B.P. (i..e kilo/1000 years before present). 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. 44º 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 ºC. Furthermore, a comparison of hypothetical sea temperatures with 17th century historical records of walrus distribution indicates that walruses in the Northumberland Strait area may have inhabited waters as warm as 18 ºC 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 (44º N) off Nova Scotia (Allen 1880; 1930) and possibly the Orkney Islands in Scotland (59º N**)** (Ray 1960). During the 16th -18th centuries, walruses used several *uglit* in the Gulf of St. Lawrence and Sable Island regions between ca. 44º – ca. 50º N (reviewed in 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).

Based on these evidences we agree with Ray (1960) and Deméré (1994) that the walrus has not evolved as cold water (Arctic) species, and that the historical range of walruses indicate that they are well adapted to cope with condition that are warmer than experienced nowadays in areas occupied by this species..

## The challenges to walruses of a warming Arctic!

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 (*O. r. divergens*) 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) increased to 15-20% (Levermann et al. 2004a). 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. 2004a). Thus, 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 and Wiig 1994). We cannot exclude that such groups are more dependent on resting on ice flows in foraging areas than adult males.

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 for 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 above 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 (Levermann et al. 2004b; Born & Acquarone 2005), 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. 2003). 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 (1956) noted that walruses in this area is benefited from the milder winters (i.e. in the 1940s and early 1950s) because the fast ice edge was closer to the shore and therefore they could eat at the mollusk banks throughout the winter. By being able to forage inshore for longer, 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 ecosystems will be a decline in benthic biodiversity 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. I 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 (Born & Knutsen 1992; Wiig et al. 1996a; Born & Acquarone 2005). 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.

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 studies of walruses in Young Sound Northeast Greenland the maximum number seen on one occasion at the houl-out at Sand Island in late July and August in the period 1998-2003 varied from year to year (1998: 28, 1999:9, 2000: 22, 2001: 19, 2002: 19, 2003: 37; 2004: 60 (Born & Acquarone 2005; 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 the summers of 2002-2004, eastern Greenland had an exceptional shortage of sea ice (L.Toudal, Technical University of Denmark, DTU, pers. comm.; Born pers. obs.). 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 (Born et al. 1997). Apparently the number of walruses using the Sand Island haul-out reflected the amount of ice in the area.

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 relatively long ice-free period in latitudes of 55-60º N where surface water temperatures are ca. 10 ºC during August (Fay & Ray 1968; Overland et al. 1999).

## Evaluation

Atlantic walruses 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. 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 ºC exclude most boreal species and only species capable of reproducing at lower temperatures inhabit arctic waters (Thorson 1933, 1934a,b). Cold-water mollusks tolerate a wide range of marine conditions: long winters with negative temperatures and seasonally varying salinities. They need <10 ºC water for reproduction and do not survive where summer temperatures exceed 20 ºC (optimum temperatures for reproduction of boreal species lie mostly between 5 and 15 ºC; Bousfield 1960). Hence, under warmer conditions, boreal bivalve species may expand their range northwards, as they did during the post-glacial warm period 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 increase. 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.” The population size of walruses in most areas of the North Atlantic are probably still far below the carrying capacity of their environment. Thus, sufficient food resources are assumed to be available as long as all traditional feeding areas still will be available in spite of the lack of ice flows to rest on.

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 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 is difficult to assess.

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 increase. A correlation between climatic amelioration and walrus catch has already been noted in West Greenland, where the catch increased markedly between 1920-1940, a period when water temperatures increased ( Born et al 1997; Førland et al. 2002). 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. 1990 a,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. 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's 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 -20º C and +15º 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 (58º 30´ N, 160º W; i.e. same latitude as northern tip of Scotland) in June, under clear skies and in 14º 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 hauled out on the Sand Island (ca. 74º N) in 1998-2000 in air temperatures up to 17 ºC (wind speed: 2-2.5 m/s) (Levermann et al. 2004a). However, 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, we 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, in certain areas 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 local walrus populations that might come from a milder Arctic climate.

## References

Allen, J.A. 1880: History of North American Pinnipeds. U.S. Geological and Geographical Survey of the Territories. Miscellaneous Publications No. 12: 785 pp.

Allen, G.M. 1930: The walrus in New England. Journal of Mammalogy 11: 139-145.

Anon. 1990a: Environmental protection. Report of working group 11, pp. 67-70 *In:* F.H. Fay, B.P. Kelly & B.A Fay (Eds.). The ecology and management of walrus populations. Report of an international workshop, 26-30 March 1990, Seattle, Washington, U.S.A. Final report to the U.S. Marine Mammal Commission in fulfillment of Contract T 68108850: 186 pp.

Anon. 1990b: Walrus, pp. 71-81 *In*: R. Hansson, P. Prestrud & N.A. Øritsland (Eds.). Assessment system for the environment and industrial activities in Svalbard. Norwegian Polar Institute: 267 pp.

Bernard, F.R., S.M. McKinnell & G.S. Jamieson 1991: Distribution and zoogeography of the Bivalvia of the eastern Pacific Ocean. Canadian Special Publication of Fisheries and Aquatic Sciences 112: 1-60; *fide* Dyke et al. 1996.

Berta, A. & J.L. Sumich 1999: Marine Mammals: Evolutionary Biology. Academic Press, San Diego, San Francisco, New York, Boston, London, Sydney, Tokyo: 494 pp.

Born, E.W. 1987: Aspects of present-day maritime subsistence hunting in the Thule area, Northwest Greenland, pp. 109-132. *In:* L. Hacquebord and R. Vaughan (Eds.). Between Greenland and America. Cross cultural contacts and the environment in the Baffin Bay area. Works of the Arctic Centre No. 10. Arctic Centre. University of Groningen. CIP-Gegevens Koninklijke Bibliotheek, Den Haag, The Netherlands: 151 pp.

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.

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: 33 pp.

Born, E.W., I. Gjertz & R.R. Reeves 1995. Population Assessment of Atlantic Walrus. Norsk Polarinstitutts Meddelelser 138: 1-100.

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.

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. *Meddelelser om Grønland Bioscience* In press

Bosscha Erdbrink, D.P. & P.H.J. Bree van 1999: Fossil cranial walrus material from the North Sea and the estuary of the Schelde (Mammalia, Carnivora). Beaufortia 49: 1-9.

Bousfield, E.L. 1960: Canadian Atlantic sea shells. National Museum of Canada. Queen´s Printer, Ottawa: 72 pp.

Bousfield, E.L. & M.L.H. Thomas 1975: Postglacial changes in distribution of littoral marine invertebrates in the Canadian Atlantic region. Proceedings Nova Scotian Institute of Science 27, Supplement 3: 47-60*; fide* Miller 1997.

Brey, T. & D. Gerdes 1998: High Antarctic macrobenthic community production. Journal of Experimental Marine Biology and Ecology 231:191-200.

Brodie, P.F. 2000: Field studies of the comparative mechanics of skin and blubber from walrus (*Odobenus rosmarus rosmarus*), pp. 339-344. *In:* J.-M. & V. de Buffrénil (Eds.). Secondary adaptations of terapods to life in the water. Verlag Dr. Friedrich Pfeil, München: 367 pp.

Deméré, T.A. 1994. The family Odobenidae: A phylogenetic analysis of fossil and living taxa, pp. 99-123. *In:* A. Berta & T.A. Deméré (Eds.). Contributions in Marine mammal Paleontology Honoring Frank C. Whitmore, Jr. Proceedings of the San Diego Society of Natural History 29: 268 pp.

Derocher, A.E., N.J. Lunn & I. Stirling 2004: Polar bears in a warming climate. Integrated and Comparative Biology 44: 163-176.

Dyke, A.S., J.E. Dale & R.N. McNeely 1996. Marine molluscs as indicators of environmental change in glaciated North America and Greenland during the last 18 000 years. Géographie physique et Quaternaire 50: 125-184.

Dyke, A.S., J. Hooper, C. R. Harington & J.M. Savelle 1999: The late Wisconsinan and Holocene record of walrus (*Odobenus rosmarus*) from North America: A review with new data from Arctic and Atlantic Canada. Arctic 52(2): 160-181.

Fay, F.H. 1960: Structure and function of the pharyngeal pounches of the walrus (*Odobenus rosmarus* L.). Mammalia 24: 361-371.

Fay, F.H. 1982: Ecology and Biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North American Fauna No. 74. U.S. Department of the Interior Fish and Wildlife Service: 279 pp.

Fay, F.H. 1960 & C. Ray 1968: Influence on climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). I. Evidence from termoregulatory behavior. Zoologica. New York Zoological Society 53: 1-14, plates I-IV.

Fay, F.H., B.P. Kelly & J.L. Sease 1989: Managing the exploitation of Pacific walruses population: A tragedy of delayed response and por communication. Marine Mammal Science 5:1-16.

Fay, F.H., J.L. Sease & R.L. Merrick 1990: Predation on a ringed seal, *Phoca hispida*, and a black guillemot, *Cepphus grylle*, by a Pacific walrus, *Odobenus rosmarus divergens*. Marine Mammal Science 6: 348-350.

Fay, F.H., L.L. Eberhardt, B.P. Kelly, J.J. Burns & L.T. Quakenbush 1997: Status of the Pacific walrus population, 1950-1989. Marine Mammal Science 13: 537-565.

Fordyce, R.E. 1980: Whale evolution and Oligocene Southern Ocean environments. Paleogeography, Paleoclimatology, Paleoecology 31: 319-336.

Fordyce, R.E. 2002: Fossil record, pp. 453-471. *In:* W.F. Perrin, B. Würsig & J.G.M. Thewissen (Eds.). Encyclopedia of marine mammals. Academic Press, San Diego, San Francisco, New York, Boston, London, Sydney, Tokyo: 1414 pp.

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

Freuchen, P. 1935: Mammals, Part II. Field notes and personal observations. Report of the Fifth Thule Expedition, 1921-1924, 2 (2-5): 68-278.

Gjertz, I. & Ø. Wiig, Ø. 1994: Past and present distribution of walruses in Svalbard. Arctic 47: 34-42.

Hall, C.A. 1964: Shallow-water marine climates and molluscan provinces. Ecology 45: 226-234; *fide* Dyke et al. 1996.

Hassol, S.J. 2004: Impacts of a warming Arctic. Cambridge University Press: 139 pp.

Henshaw, A. 2003: Polynyas and ice edge habitats in cultural context: Archaeological perspectives from Southeast Baffin Island. Arctic 56: 1-13.

Hills, S. 1992: The effect of spatial and temporal variability on population assessment of Pacific walruses. PhD-thesis, University of Maine, Orono, December 1992: 120 pp.

Kelly, B.P. 2001: Climate change and ice breeding pinnipeds, pp. 43-55. *In:* G.-R. Walther et al. (Eds.). Fingerprints of climate change. Kluwer Academic/Plenum Publishers, New York: 338 pp.

Kiliaan, H.P.L. & I. Stirling 1978: Observations of overwintering walruses in the eastern Canadian High Arctic. Journal of Mammalogy 59: 197-200

Klages, M., A. Boetius, J.P. Christensen, H. Deubel, D. Piepenburg, I. Schwede & T. Soltwedel 2004: The benthos of Arctic seas and its role for the organic carbon cycle at the seafloor, pp. 139-167. *In:* R. Stein & R.W. Macdonald (Eds.). The organic carbon cycle in the Arctic Ocean. Springer Verlag, Berlin, Heidelberg: 263 pp.

Levermann, N., M.C. Forchhammer, M. Acquarone & E.W. Born, 2004a. Climate and density dependent haul-out dynamics in walruses. In preparation for Can J Zool. Chapter IV. *In:* N. Levermann: Waltzing with walruses. M.Sc. thesis, November 2004, University of Copenhagen: 141 pp.

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

Lowry, L.F. & F.H. Fay 1984: Seal eating by walruses in the Bering and Chukchi Seas. Polar Biology 3: 11-18.

Miller, R.F. 1997: New records and AMS radiocarbon dates on Quaternary walrus (*Odobenus rosmarus*) from New Brunswick. Géographie physique et Quaternaire 51: 1-5.

Overland, J.E., S.A. Salo, L.H. Kantha & C.A. Clayson 1999: Thermal straticfication and mixing on the Bering Sea shelf, pp. 129-146. *In:* T.R. Loughlin & K. Ohtani (Eds.). Dynamics of the Bering Sea: A Summary of Physical, Chemical, and Biological Characteristics, and a Synopsis of Research on the Bering Sea. University of Alaska Sea Grant, AK-SG-99-03, North Pacific Marine Science Organization (PICES): 825 pp.

Ray, C.E. 1960: *Trichecodon huxlei* (Mammalia: Odobenidae) in the Pleistocene of southeastern United States. Bulletin of the Museum of Comparative Zoology at Harvard College 122: 129-142; 2 Plates.

Ray, C. & F.H. Fay 1968: Influence on climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). II. Evidence from physiological characteristics. Zoologica. New York Zoological Society 53: 19-32.

Repenning, C.A., C.E. Ray & D. Grigorescu 1979: Pinniped Biogeography, pp. 357-369. *In:* J. Grey & A.J. Boucot (Eds.). Historical biogeography, plate tectonics and the changing environment. Oregon State University Press, Corvalis, Oregon. 500 pp.

Rysgaard, S., T. G. Nielsen & B.W. Hansen 1999: Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. Marine Ecology Progress Series 179: 13-25.

Rysgaard, S., T. Vang, M. Stjernholm, B. Rasmussen, A. Windelin & S. Kiilsholm 2003: Physical conditions, carbon transport, and climate change impacts in a Northeast Greenland Fjord. Arctic, Antarctic, and Alpine Research 35: 301-312.

Salter, R.E. 1980: Observations on social behaviour of Atlantic walruses (*Odobenus rosmarus* (L.)) during terrestrial haul-out. Canadian Journal of Zoology 58: 461-463.

Sejr, M.K., K.T. Jensen & S. Rysgaard 2000: Macrozoobenthic community structure in a high-arctic East Greenland fjord. Polar Biology 23: 792-801.

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

Stabeno, P.J. & J.E. Overland 2001. Bering Sea shifts toward an earlier spring transition. EOS, Transactions of the American Geophysical Union 82: 317-321.

Stanley, S.M. 1989: Earth and life through time. 2nd Edition. W.H. Freeman, New York: 689 pp.

Stirling, I. 1984: A group threat display given by walruses to polar bear. Journal of Mammalogy 65: 352-353.

Thorson, G. 1933: Investigations on shallow water animal communities in the Franz Joseph Fjord (East Greenland) and adjacent waters. Meddelelser om Grønland 100(2): 1-70 + 3 plates.

Thorson, G. 1934a: Contributions to the animal ecology of the Scoresby Sound Fjord complex (East Greenland). Meddelelser om Grønland 100(3): 1-67.

Thorson, G. 1934b: Marine molluscs. Meddelelser om Grønland 104(17): 1-8.

Vibe, C. 1950: The marine mammals and the marine fauna in the Thule District (Northwest Greenland) with observations on the ice conditions in 1939-41. Meddelelser om Grønland 150: 1-115.

Vibe, C. 1956: Thule and Scoresbysund - Grønlands to nordligste fangst-distrikter (Thule and Scoresbysund - the northernmost hunting districts in Greenland). Tidsskriftet Grønland 11: 415-427.

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

Wiig, Ø., S.E. Belikov, A.N. Boltunov & G.N. Garner 1996b. Selection of marine mammal valued ecosystem components and description of impact hypotheses in the Northern Sea Route Area. INSROP Working Paper No. 40, II.4.3: 1-73.

Wlodarska-Kowalczuk, M. & J.M. Weslawski 2001: Impact of climate warming on Arctic benthic biodiversity: a case study of two Arctic glacial bays. Climate Research 18: 127-132.

Zubakov, V.A. & I.I. Borzenkova 1988: Pliocene paleoclimates: Past climates as possible analogues of mid-twenty-first century climate. Paleogeography, Paleoclimatology, Paleoecology 65: 35-49.