

An assessment of Greenland walrus populations

Lars Witting and Erik W. Born

Witting, L., and Born, E. W. 2005. An assessment of Greenland walrus populations. — ICES Journal of Marine Science, 62: 266–284.

Recent abundance estimates were combined with historical catches and an age- and sex-structured population dynamic model to perform Bayesian assessments of the walrus (*Odobenus rosmarus*) populations in West Greenland, the North Water in northern Baffin Bay, and East Greenland. The model assumed density-regulated dynamics and pre-harvest populations in population-dynamical equilibrium. It projected the populations under the influence of the catches to estimate the historical trajectories and the current population status. It was found that the West Greenland and North Water populations have been heavily exploited during the last century with the current abundance being at best only a few per cent of the historical abundance. Apparently these populations are still being exploited above sustainable level. The East Greenland population was heavily exploited after 1889 and during the first half of the 20th century and was depleted to approximately 50% of pristine population size in 1933. After protective measures were introduced in the 1950s this population has increased to a current level close to the abundance in 1889, and the present exploitation appears to be sustainable.

© 2004 International Council for the Exploration of the Sea. Published by Elsevier Ltd. All rights reserved.

Keywords: Bayesian statistics, density regulation, Greenland, marine mammal, modelling, *Odobenus rosmarus*, population dynamics, sustainable exploitation, walrus.

Received 16 March 2004; accepted 5 November 2004.

L. Witting and E. W. Born: Greenland Institute of Natural Resources, PO Box 570, DK-3900 Nuuk, Greenland. Correspondence to L. Witting: tel: +299 361200; fax: +299 361212; e-mail: larsw@natur.gl.

Introduction

The management of an exploited population of wild animals is often faced with the dilemma between incomplete knowledge on the dynamics and status of the population and the need to determine sound levels of exploitation. If knowledge was complete the implications of a given harvest could be calculated exactly, and it would be relatively easy to set the exploitation to a level where management objectives would be met. In reality, however, the uncertainty trade-off implies that a given harvest can at best be associated with a certain probability that the management goals for the population will be met. In this paper we apply a Bayesian statistical model to the incomplete data on the three exploited populations of Atlantic walrus (*Odobenus rosmarus rosmarus*) in Greenland, in order to estimate the historical development of the populations, their current status, and sustainable exploitation levels.

The three populations of Atlantic walrus in West, Northwest, and East Greenland have been subject to exploitation for centuries. First at a limited scale by Inuit and then by European whalers and sealers, who tolled heavily on the populations. From the beginning of the 20th

century Greenlanders hunted walrus with increasing efforts after the introduction of fire-arms and motorized vessels. The populations are still exploited for subsistence purposes, and for some there are indications of over-exploitation (Born *et al.*, 1995; NAMMCO, 1995). Hence, it seems warranted to attempt an assessment of the present status of the Greenland walrus populations in the light of historical and current exploitation.

The “West Greenland” population of walrus occurs from fall to spring at the edge of the Baffin Bay pack ice from c. 66°30'N to 70°30'N (Born *et al.*, 1994, 1995; Figure 1). Further north in Baffin Bay and Smith Sound walruses occur almost year-round in the North Water polynya and adjacent areas. They are, however, absent from the coastal areas of NW Greenland during the open water season in August–September when they summer along the eastern and southern coast of Ellesmere Island (Canada) and in the Canadian High Arctic archipelago (Born *et al.*, 1995). Walruses in these areas are referred to as “the North Water” population (Born *et al.*, 1995). Walruses occur year-round along the eastern coast of Greenland where they mainly are distributed inside the National Park of North and Northeast Greenland north of the entrance to Scoresby Sound (c. 71°N) (Born *et al.*, 1995, 1997). There is only

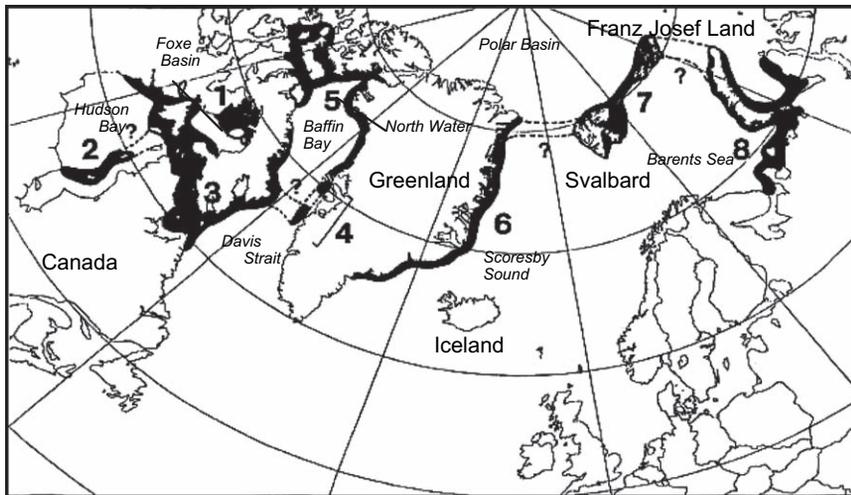


Figure 1. The distribution of putative sub-populations of Atlantic walrus (Born *et al.*, 1995). The three Greenland walrus populations that were dealt with during this study are numbered 4 (West Greenland), 5 (North Water), and 6 (East Greenland). Question marks indicate a potential connection between West Greenland (4) and Canadian walruses (3), and East Greenland (6) and Svalbard-Franz Josef Land (7) walruses. The other sub-populations are: (1) Foxe Basin, (2) Southern and Eastern Hudson Bay, (3) Northern Hudson Bay-Hudson Strait-Southeastern Baffin Island, (7) Svalbard-Franz Josef Land, and (8) Kara Sea-Southeastern Barents Sea-Novaya Zemlya.

limited exchange between the East Greenland and neighbouring populations, i.e., West Greenland, North Water, and the Svalbard-Franz Land populations (Born *et al.*, 1995, 2001; Andersen *et al.*, 1998).

Information on distribution and migration (Born *et al.*, 1994, 1995, 1997) and genetics (Andersen *et al.*, 1998; Andersen and Born, 2000; Born *et al.*, 2001) indicates that the three Greenland walrus populations represent separate population units and therefore should be managed separately (NAMMCO, 1995). Currently, however, there are no management plans or objectives for the exploitation of walruses in Greenland.

For the depleted population of beluga (*Delphinapterus leucas*) in West Greenland a management scheme or objective has been suggested that allows the population to increase (NAMMCO, 2002). For populations below the maximum sustainable yield level this objective is close to that for the Greenland exploitation of large cetaceans (i.e., minke whale *Balaenoptera acutorostrata* and fin whale *Balaenoptera physalys*) that are managed by the International Whaling Commission (IWC). For the aboriginal whaling in Greenland the IWC Schedule (IWC, 2000) states that catches shall be permitted from populations below the maximum sustainable yield level (msyl) as long as the population is above a protection level and the exploitation allows the population to increase toward the msyl. For populations at or above the msyl catches shall be permitted as long as the total removals do not exceed 90% of the maximum sustainable yield (msy). For the purpose of this study we provisionally adopt this management objective, except that we do not specify a protection level.

Previous attempts to model walrus populations include the use of discrete population models to simulate

population dynamics of a hypothetical walrus population (DeMaster, 1984; Chivers, 1999). Simple recursive models (Born *et al.*, 1997; Gjertz *et al.*, 1998) have also been used to back-calculate the size of the East Greenland and Franz Josef Land walrus populations, respectively. By combining crude estimates of population size with estimates of current levels of exploitation it was attempted in 1995 to determine the status of the Greenland walrus populations (Born *et al.*, 1995; NAMMCO, 1995).

In this paper we summarize the walrus catch history for the West Greenland, the North Water, and the East Greenland populations for the last century. In the case of the West Greenland population we extrapolated the catch history back to 1820 to investigate the effects on current population status of the length of the period of exploitation. We applied this information, and recent abundance estimates, in a density regulated model with age and sex structure to (i) reconstruct the historical dynamics of the three populations, (ii) evaluate their current status, and (iii) determine sustainable yield levels.

The assessment model applied is based on a Bayesian statistical method (Berger, 1985; Press, 1989; Punt and Hilborn, 1997; McAllister and Kirkwood, 1998). Bayesian assessments have recently been applied to marine mammals like the bowhead whale (*Balaena mysticetus*) in the Bering-Chukchi-Beaufort Seas (Givens *et al.*, 1995; Raftery *et al.*, 1995), the gray whale (*Eschrichtius robustus*) in the eastern Pacific (Wade, 2002; Witting, 2003), and beluga (*Delphinapterus leucas*) in Baffin Bay (Innes and Stewart, 2002; Alvarez-Flores and Heide-Jørgensen, 2004) and they are particularly useful when faced with limited or uncertain information on the stocks in question.

Method

Model runs

The assessment of Greenland walrus was based on five runs of the Bayesian assessment model. The first three runs were comparable assessments for the three populations based on catch histories from about 1900. Although these catch histories may be considered best estimates, they are not complete because walrus were taken from all three populations earlier than 1900. A sensitivity run was therefore applied to the West Greenland population where it was possible to provide crude estimates of the catches back to 1820. All these runs were based on the assumption of an even sex ratio at birth (Fay, 1982; Born, 2001). There are, however, some indications that at least Pacific walrus (*O. r. divergens*) may have female biased sex ratios in the breeding population (e.g., Fay *et al.*, 1997). A second sensitivity test was therefore applied to the West Greenland population where the sex ratio at birth was set to the sex ratio in the harvest which apparently had a ratio of 0.4M:0.6F (Born *et al.*, 1994).

Data

Estimates of current abundance, catches, and losses are described for each population separately.

Current abundance

West Greenland. The point estimates obtained from aerial surveys during late March 1990 and early April 1991 of the visible portion of the population in West Greenland were 458 and 631, respectively (mean: 545). About 18% of the walrus observed were in the water and the remainder on the ice (Born *et al.*, 1994). Walrus in water usually spend about 20% of the time at the surface (i.e. upper 0–2 m) (Fay, 1982; Wiig *et al.*, 1993; Born and Knutsen, 1997; Born *et al.*, 2003). If applying a correction factor (i.e. four walrus submerged for every walrus seen in the water) to the mean of the number of walrus in the water (98), the estimate of the total number of walrus that were in the water is 491. By adding this to the number on the ice (447), the estimate of the West Greenland stock is 938, with a CV of 0.48 based on the survey data.

North Water. In order to enumerate the number of walrus in the North Water population, the Department of Fisheries and Oceans (DFO, Winnipeg, Canada) and the Greenland Institute of Natural Resources (GINR, Nuuk, Greenland) jointly conducted an aerial survey during 11–19 August 1999 over terrestrial walrus haul-outs and along the coasts on eastern Ellesmere Island and in the Jones Sound, south Devon Island, and Cornwallis Island-Grinnell Peninsula areas in Canada (DFO and GINR, unpublished data; Dunn, 2000). These are the main summering areas of walrus in the North Water population (Born *et al.*, 1995).

If the maximum counts per area are summed, a total of 452 walrus was observed, of which 73.5% were hauled out. In the Jones Sound and Cornwallis Island-Grinnell Peninsula areas, which were surveyed twice, the minimum

counts obtained during one survey were 71% and 83%, respectively, of the maximum counts of the other survey.

These aerial survey counts were corrected in two alternative ways: (i) The number of walrus at sea (120) was multiplied by 5 to include the number that theoretically was submerged (i.e. 80%). The total number of walrus at sea (i.e. 600) was then added to the actual number observed on land (332). (ii) The number observed hauled out (=30%, e.g., Born and Knutsen, 1997; Born and Acquarone, 2005) was simply multiplied by 3.3 to include the fraction not present at the haul-outs.

The resulting estimates of the total number of walrus in the North Water population were (i) 932 and (ii) 1097, indicating that about 1000 walrus were within the surveyed areas during the period 11–19 August 1999. To include walrus in areas not surveyed (southern coasts of Lancaster Sound and Barrow Strait and adjacent areas, and a section of eastern Ellesmere Island where walrus may occur sometimes), this estimate was raised to 1500 for the simulations and the CV of this estimate was arbitrarily set to 0.35 (this CV allows for inclusion of the plausible ranges of the estimate of abundance).

East Greenland. Based on opportunistic and systematic observations, the East Greenland walrus population was estimated to number ca. 1000 (Born *et al.*, 1997). The CV was set to 0.35 for the same reason as given for the North Water population.

Catch data and loss rates

Two catch histories were estimated for each population. A “low” catch history based on reported or landed catch (and in some years estimates of the catch) and a “high” catch history that includes also estimates of non-reported loss, i.e., animals that were struck and lost, and animals that were landed and not reported.

West Greenland. Catch data were extracted from official catch statistics and written sources (Born *et al.*, 1994), and sources given in Table 1.

Losses were assumed to average 10% (1 lost for every 10 killed) from 1900 until 1930. During this period walrus were mainly taken by traditional means close to the coast and primarily at the terrestrial haul-outs. From 1930 onwards when walrus increasingly were hunted by use of motorized vessels operating in the offshore pack ice (Born *et al.*, 1994) losses were assumed to average 25% (1 lost for every 4 killed). Loss rates of 20–30% are not uncommon during walrus hunts based on small-type vessels (cf. Born *et al.*, 1995 and references therein; Gjertz *et al.*, 1998).

We assumed an even sex ratio in the catch before 1930, while an estimated sex ratio of M:F = 0.4:0.6 was applied to the catch history after 1930 (Born *et al.*, 1994).

North Water. Generally, the catch data from the Thule area of NW Greenland are insufficient in particular prior to 1950

Table 1. The reported catch (in some cases estimated catch) of walrus in West Greenland, 1900–1999. The numbers represent the “low” catch history used in the modelling of the population; i.e., without loss.

Year	Catch	Year	Catch	Year	Catch	Year	Catch
1900	10 ¹	1925	70	1950	38 ³	1975	81
1901	10 ¹	1926	165	1951	280 ⁴	1976	101
1902	69 ²	1927	135	1952	280 ⁴	1977	47
1903	3	1928	280	1953	280 ⁴	1978	59
1904	79 ²	1929	165	1954	286	1979	72
1905	200	1930	245	1955	198	1980	54
1906	84 ²	1931	180	1956	410	1981	74
1907	107	1932	325	1957	202	1982	61
1908	43 ²	1933	85	1958	194	1983	54
1909	49 ²	1934	70	1959	351	1984	58
1910	11	1935	95	1960	114	1985	51
1911	50	1936	465	1961	122	1986	34
1912	15 ²	1937	540	1962	115	1987	61
1913	25	1938	625	1963	53	1988	58 ⁶
1914	100	1939	522	1964	71 ⁵	1989	58 ⁶
1915	60	1940	621	1965	45	1990	58 ⁶
1916	100	1941	543	1966	41	1991	58 ⁶
1917	12	1942	316	1967	19	1992	58 ⁶
1918	15	1943	301	1968	32	1993	241 ⁷
1919	215	1944	269	1969	98	1994	243
1920	30	1945	444	1970	36	1995	265
1921	50	1946	494	1971	45	1996	176
1922	60	1947	331	1972	59	1997	242
1923	193	1948	268	1973	60	1998	174
1924	50	1949	96 ⁴	1974	50	1999	184

Sources: 1) Estimate. 2) Estimate inferred from trade in tusk ivory (Vibe, 1967; Figure 45); kg ivory was converted to individual walrus by using data in Chapskii (1936) on ivory mass per walrus; females = 0.7 kg individual⁻¹; males = 0.9 kg individual⁻¹ 3) Incomplete reporting; not corrected. 4) Average of catch reported during 1945–1954. 5) Estimate; average of catch reported during the 1960s. 6) No reporting; average of previous 10 years (1978–1987). 7) New system of reporting (called “Piniameq”) from 1993.

(Teilmann and Kapel, 1998). Hence, to obtain estimates for the early period, catches were inferred from the trend in growth of the human population in the area. Inferred from Gilberg (1976; Figure 19), the Inuit population in the Thule area increased gradually with a rate of ca. 0.8% per year from about 200 at 1900 to about 300 around 1950. If assuming a proportional relationship between (i) the size of the human population, (ii) the fraction of hunters (29–34% of the human population were men aged 15–64 years; Gilberg (1976; Table 25)) in this population, and (iii) the number of walrus caught per hunter, the annual catch of walrus during the year 1900–1950 was back-calculated from an average of about 200 in 1939–1940 (Vibe, 1950): Catch (c) in year $x - 1 = c_x \cdot 0.9918$; Table 2.

Losses were assumed to average 5% from 1900 until 1950. During this period walrus were mainly taken by

traditional means and only few motorized vessels were available for hunting. Furthermore, the walrus were harpooned before being shot. For the period 1951–1969, a loss rate of 15% was applied taking into account an increased use of vessels during the open water period where walrus hauling out on ice floes can be shot at before they are harpooned. After 1970, an overall loss rate of 25% (1 lost for every 4 killed) was used based on observations in the late 1970s (Born *et al.*, 1995).

An age-structured catch (Table 3) is available from a sample of the Greenlanders catch of walrus (0–29 years of age) in the North Water (1987–1991). The sex ratio in this sample (F: $n = 179$; M: $n = 197$), which did not differ from unity ($\chi^2 = 0.43$, $p = 0.512$, d.f. = 1), was applied to the catch history for the entire period.

East Greenland. Catches in East Greenland were extracted from Born *et al.* (1997); Table 4. An average loss rate of 20% was applied to the catch by the European sealing vessels (Chapskii, 1936; Gjertz *et al.*, 1998). An overall loss rate of 27% and 23% was applied to the catches taken by European trappers and Greenlanders, respectively (Born *et al.*, 1997).

Information is not available on the sex ratio in the catches taken by European sealers prior to 1956 when walrus were completely protected in NE Greenland north of ca. 72°N (Born *et al.*, 1997) – effectively prohibiting the catch of walrus in East Greenland by foreigners. Hence, for the period 1889–1955 an even sex ratio in the catch was assumed. South of 72°N the Greenlanders’ recent catch consists of ca. 90% male walrus (Born *et al.*, 1997), and we therefore applied a 0.9M:0.1F ratio for the catch in East Greenland after 1956.

Population dynamic model

An age- and sex-structured model with direct density regulation on the birth rate is applied. The number of animals in age classes larger than zero is

$$\begin{aligned} N_{t+1,a+1}^{m/f} &= (N_{t,a}^{m/f} - C_{t,a}^{m/f})s_a \quad 0 \leq a \leq x - 2 \\ N_{t+1,x}^{m/f} &= (N_{t,x}^{m/f} - C_{t,x}^{m/f})s_x + (N_{t,x-1}^{m/f} - C_{t,x-1}^{m/f})s_{x-1} \end{aligned} \quad (1)$$

where $x = 15$ is the lumped age class of animals 15 years and older, $N_{t,a}^{m/f}$ is the number of males/females of age a at the start of year t , $C_{t,a}^{m/f}$ is the catch of males/females of age a during year t , with the age distribution of the catches being sex-specific and proportional to the product between the age- and sex-specific abundance $N_a^{m/f}$ and an age- and sex-specific catch selectivity factor $c_a^{m/f}$. The proportionality of the age-structured catch to the product $N_a^{m/f} C_a^{m/f}$ can be obtained for all age classes only when the total catch is so low that the catch from any sex-specific age class does not exceed the abundance in that class. If instead the estimated catch exceeds the abundance in an age class, the catch in that age class is set to the

Table 2. The reported (and estimated) retrieved catch of walrus by Greenlander and others from the North Water population, 1900–1999. The numbers represent the “low” catch series; i.e., without loss.

Year	Green	Other	Year	Green	Other	Year	Green	Other	Year	Green	Other
1900	145 ¹	10 ²	1925	178	10	1950	132 ⁵	76	1975	130	23
1901	146	10	1926	180	10	1951	23 ⁸	1251 ⁷	1976	124 ¹⁰	23
1902	147	10	1927	181	10	1952	64 ⁹	76 ¹²	1977	230 ¹⁶	23
1903	149	10	1928	183	10	1953	48	76	1978	230	23
1904	150	10	1929	184	10	1954	42	76	1979	150 ¹⁷	23
1905	151	10	1930	186	10	1955	195	76	1980	150	23
1906	152	10	1931	187	10	1956	119	16 ¹³	1981	188	23
1907	154	10	1932	189	10	1957	196	16	1982	170	23
1908	155	10	1933	190	10	1958	290 ¹⁰	16	1983	162	23
1909	156	10	1934	192	57 ⁶	1959	132 ⁵	16	1984	244	23
1910	158	10	1935	194	57 ⁶	1960	132 ⁵	16	1985	80	20 ²⁰
1911	159	10	1936	195	10	1961	132 ⁵	16	1986	147 ¹⁸	20
1912	160	10	1937	197	10	1962	440 ¹⁰	16	1987	147	20
1913	161	10	1938	198	10	1963	132 ⁵	15 ¹⁴	1988	147	21 ²¹
1914	163	10	1939	200 ³	10	1964	132 ⁵	15	1989	147	21
1915	164	10	1940	200	10	1965	132 ⁵	15	1990	147	21
1916	165	10	1941	200	10	1966	132 ⁵	15	1991	147	21
1917	167	10	1942	200 ⁴	10	1967	132 ⁵	15	1992	147	21
1918	168	10	1943	200	10	1968	132 ⁵	15	1993	265 ¹⁹	21
1919	170	10	1944	200	10	1969	132 ⁵	15	1994	156	20 ²²
1920	171	10	1945	200	10	1970	132 ⁵	15	1995	128	20
1921	172	10	1946	200	10	1971	130 ¹¹	15	1996	122	20
1922	174	10	1947	200	10	1972	130	23 ¹⁵	1997	74	20
1923	175	10	1948	132 ⁵	10	1973	130	23	1998	72	20
1924	177	10	1949	132	623 ⁷	1974	130	23	1999	101	20

Sources: 1) Catch during 1900–1938 based on back-calculation from 1939. 2) Estimated catches taken by Canadian Inuit (the Inuit population was sparse and the catch of walrus likely low). 3) For 1939–1941 estimated by Vibe (1950). 4) 1943–1947 Vibe (1950) continued. 5) 1948–1950; Mansfield (1973): Average of catch reported in Hunters Lists of Game (HLG). 6) Dundas Harbour (Born *et al.*, 1995). 7) Taken by a Norwegian vessel (unpublished information on file at the Greenland Institute of Natural Resources). 8) Estimated from amount of walrus hides traded to the Greenland Trade Department. 9) 1952–1957, estimated from amount of walrus blubber traded to the Greenland Trade Department. 10) Reported in HLG. 11) 1971–1975, estimates based on Bruemmer (1971). 12) 1952–1955, Born *et al.* (1995). 13) 1956–1962, catch in Alexandra Fjord (Born *et al.*, 1995). 14) 1963–1971, estimated (this study). 15) 1972–1984, Richard and Campbell (1988). 16) 1977–1978, Born, unpublished data (Born *et al.*, 1995). 17) 1979–1985, HLG. 18) 1986–1992, estimated based on average of catches reported during 1979–1985 and 1993–1999. 19) 1993–1999, reported in Piniarq. 20) 1985–1987, estimated (this study). 21) 1988–1993, R. E. A. Stewart in literature (Born *et al.*, 1995). 22) 1994–1999, estimated (this study).

abundance of that class, while the remaining catches are reallocated to the remaining classes in proportion to the age- and sex-specific selectivity factors and abundances. If necessarily, this redistribution of the catches continues until it is possible to redistribute the remaining catches

in an age and sex structure where the catch from any class does not exceed the number of individuals in that class.

The annual survival rate of adults (s_{ad}) applies to all animals older than two years (s_{2+}), the survival of juveniles

Table 3. The number of male (m) and female (f) walrus caught per age class in the North Water, 1987–1991, based on 376 samples. There are 49 samples from the age classes 16 to 29 that are not shown.

Age	m	f	Age	m	f	Age	m	f	Age	m	f
0	6	11	4	4	7	8	4	14	12	10	17
1	6	3	5	7	8	9	18	13	13	16	7
2	5	4	6	9	17	10	23	21	14	12	3
3	4	8	7	11	7	11	17	21	15	5	9

Table 4. The Greenland and foreign catch of walrus from the East Greenland population, 1889–1999. The numbers represent the “low” catch history used in the modelling of the population; i.e., without loss.

Year	Green	Other	Year	Green	Other	Year	Green	Other	Year	Green	Other
1889	1 ¹	267	1917	1	0	1945	1	5	1973	1	0
1890	1	0	1918	1	0	1946	1	5	1974	1	0
1891	1	0	1919	1	37	1947	3	5	1975	5	0
1892	1	0	1920	1	8	1948	2	5	1976	1	0
1893	1	0	1921	1	0	1949	3	5	1977	3	0
1894	1	0	1922	1	9	1950	1	5	1978	2	0
1895	1	0	1923	1	9	1951	1	5	1979	1	0
1896	1	0	1924	1	2	1952	1	5	1980	1	0
1897	1	23	1925	1	11	1953	1	5	1981	10	0
1898	1	134	1926	70	2	1954	2	5	1982	11	0
1899	1	89	1927	11	62	1955	13	5	1983	18	0
1900	1	42	1928	6	2	1956	3	0	1984	10	0
1901	1	76	1929	2	13	1957	1	0	1985	22	0
1902	1	30	1930	3	10	1958	2	0	1986	3	0
1903	1	23	1931	1	13	1959	2	0	1987	9	0
1904	1	10	1932	1	67	1960	1	0	1988	7	0
1905	1	22	1933	1	6	1961	1	0	1989	2	0
1906	1	53	1934	1	10	1962	1	0	1990	7	0
1907	1	4	1935	1	7	1963	1	0	1991	2	0
1908	1	79	1936	1	10	1964	1	0	1992	2	0
1909	1	5	1937	1	8	1965	1	0	1993	15 ³	0
1910	1	6	1938	1	4	1966	1	0	1994	8	0
1911	1	0	1939	1	21	1967	1	0	1995	8	0
1912	1	2	1940	1	5 ²	1968	1	0	1996	7	0
1913	1	0	1941	1	5	1969	1	0	1997	1	0
1914	1	0	1942	1	5	1970	1	0	1998	7	0
1915	1	0	1943	1	5	1971	1	0	1999	8	0
1916	1	0	1944	1	5	1972	1	0	—	—	0

Sources: 1) The Greenlanders catch during 1900–1925 was estimated. Likely, catches were low because only the Ammassalik south of the main distribution of walrus was populated until 1925. Furthermore, for all other years without reporting it was assumed that at least one walrus had been landed by Greenlanders. 2) For the period 1940–1955 (when foreign sailing vessels no longer caught walrus in East Greenland, it was assumed that Danish and Norwegian hunters and trappers living in NE Greenland landed five walruses per year (Born et al., 1997)). 3) 1993–1999, reported in Piniarneq. Clearly implausible reports in Piniarneq (i.e. 1994: 60; 1995: 46; 1999: 26) were replaced with estimates (average of other years with Piniarneq data).

during the second year (s_1) is s_{juv} , and the survival during the first year (s_0) is $s_{juv}s_{ad}$, assuming that first year survival depends also on the survival of the mother.

The number of births at the start of year t is

$$B_t = \sum_{a=a_m}^x B_{t,a}^f + B_{t,a}^m \quad (2)$$

where a_m is the age of reproductive maturity given by the first year with reproduction, and $B_{t,a}^f$ and $B_{t,a}^m$ are the number of female and male births in age class a . These births are

$$\begin{aligned} B_{t,a}^f &= \vartheta b_t \tilde{N}_{t,a}^f \\ B_{t,a}^m &= (1 - \vartheta) b_t \tilde{N}_{t,a}^f \end{aligned} \quad (3)$$

where ϑ is the fraction of females at birth, b_t is the birth rate for mature females at time t , and $\tilde{N}_{t,a}^f$ is the number of

mature females in age class a at the start of year t , defined as

$$\tilde{N}_{t,a}^f = \begin{cases} 0 & \text{if } a_m > a \\ N_{t,a}^f & \text{if } a_m \leq a \end{cases} \quad (4)$$

The component of the population that imposes density regulation is the one plus component

$$\hat{N} = \sum_{a=1}^x N_a^f + N_a^m \quad (5)$$

and the density regulation on the birth rate b_t takes the Pella-Tomlinson form

$$b_t = b^* + [b_{max} - b^*] \left[1 - (\hat{N}_t / \hat{N}^*)^z \right] \quad (6)$$

where b^* is the birth rate at population dynamic equilibrium N^* , b_{max} is the maximal birth rate, and z is the compensation parameter.

Although not explicit parameters of the model, the maximum sustainable yield level (msyl) and the maximum sustainable yield rate (msyr) are treated as parameters in the analysis. The msyl depends mainly on the compensation parameter z , and to speed computation the three parameters are defined relative to the mature component of the population, denoted by the symbol $\tilde{\cdot}$. Hence, the birth rate is

$$b = b^* + (b_{\max} - b^*)(1 - \tilde{d}^z) \quad (7)$$

where $\tilde{d} = \tilde{N}/\tilde{N}^*$ is the depletion ratio. Given no changes in the sex ratio with age, from the steady state $\tilde{N}_{t+1} = \tilde{N}_t$ with $\tilde{N}_{t+1} = \tilde{N}_t s_{\text{ad}} \theta b - s\tilde{y}$, the sustainable yield is

$$s\tilde{y} = \tilde{N}[s_m \theta b - (1 - s_{\text{ad}})] \quad (8)$$

where $s_m = \prod_{i=0}^{a_m-1} s_i$ is survival from birth to age of reproductive maturity. The $s\tilde{y}r$ relative to the depletion ratio \tilde{d} is then

$$s\tilde{y}r = \tilde{d}[s_m \theta b_{\max} - s_m \theta (b_{\max} - b^*) \tilde{d}^z - (1 - s_{\text{ad}})] \quad (9)$$

Solving $d s\tilde{y}r / d\tilde{d} = 0$ for \tilde{d} , the $m\tilde{s}y$ l is

$$m\tilde{s}y\text{l} = \left[\frac{s_m \theta b_{\max} - (1 - s_{\text{ad}})}{s_m \theta (b_{\max} - b^*)(1 + z)} \right]^{1/z} \quad (10)$$

with the $m\tilde{s}y$ r being the $s\tilde{y}r$ at the $m\tilde{s}y$ l.

Statistical methods

The model was fitted to the abundance estimate by projecting the population from the first year with harvest under the influence of the historical catches, assuming that the pre-harvested population was in dynamic equilibrium. A Bayesian statistical method (e.g., Berger, 1985; Press, 1989) was used, and posterior estimates of the model parameters and other management related outputs were calculated. This implied an integration of the product between a prior distribution for each parameter and a likelihood function that links the probability of the data to the different parameterizations of the model.

The method of De la Mare (1986) was used to calculate the likelihood L under the assumption that observation errors are lognormally distributed (Buckland, 1992)

$$L = \prod_t \exp\left(-\frac{[\ln(N_t^i/N_t)]^2}{2CV_t^2}\right) / CV_t \quad (11)$$

where N_t is the projected and N_t^i the point estimate of the observed total abundance at time t , and CV_t is the coefficient of variation of the abundance estimate at time t .

The integration was obtained by the sampling-importance-resampling routine (Berger, 1985; Rubin, 1988), where $n_1 = 2\,000\,000$ random parameterizations $\theta_i (1 \leq i \leq n_1)$ were sampled from an importance function $h(\theta)$ (Oh and Berger, 1992; McAllister *et al.*, 1994; McAllister and Ianelli, 1997). The importance function was set to the joint prior, so

that the importance weight is given simply by the likelihood. To generate a random sample of the posterior distribution, the n_1 parameter sets were then resampled $n_2 = 5000$ times with replacement, with the sampling probability of the i (th) parameter set being

$$q_i = \frac{w(\theta_i)}{\sum_{j=1}^{n_1} w(\theta_j)} \quad (12)$$

If the importance function is adequately specified, the mean of the importance sample for each parameter should approach the mean from the true posterior distribution, given a sufficiently large sample. To illustrate whether the sampled posterior quantities can be assumed to be representative of the true posterior distribution, convergence diagnostics were calculated. One such diagnostic is the maximum importance weight of a parameter set relative to the total summed importance weight over all n_1 draws. For example, McAllister *et al.* (2001) suggest that the maximum importance weight needs to have dropped below 1% of the total sum. And in line with Wade (2002), we also calculated the total number of unique parameter sets in the resample of n_2 parameter sets, as well the maximum number of occurrences of a unique parameter set in the resample.

Probability of meeting the objective

Given future annual catches c in the period 2005–2009, we applied the objective

$$\text{ob} = \begin{cases} N_{2010} > N_{2005} & \text{if } N_{2005} < N^* \text{ msyl} \\ c \leq 0.9 \text{ msy} & \text{if } N_{2005} \geq N^* \text{ msyl} \end{cases} \quad (13)$$

Given the population dynamic model and the data, the probability of meeting the objective (ob) is straightforwardly calculated from the Bayesian statistical method. For each parameterization θ_i of the random sample of the posterior distribution of size n_2 , we have perfect knowledge of the status of the population so that it can be determined if Equation (13) is true or false. Hence, the probability $p(\text{ob})$ of meeting the objective is

$$p(\text{ob}) = \sum_{i=1}^{n_2} g(\theta_i, c) / n_2 \quad (14)$$

$$g(\theta_i, c) = \begin{cases} 1 & \text{if ob is true} \\ 0 & \text{if ob is false} \end{cases}$$

with the sum given over the complete random sample of the posterior distribution.

Age-selective catch

Assuming that the age- and sex-specific catch selectivity factor $c_a^{m/f}$ increases linearly with age from age class zero to x , and that it remains constant thereafter, it follows that the complete age selectivity curve is described by the selectivity ratio c_0/c_x . Given this model and an assumed

stable age structure, the catch will decline with age for $a \geq x$. For the age- and sex-structured catch in the North Water during 1987–1991 (Table 3), this decline begins from age class 10 in both males and females, suggesting a similar catch pattern for both sexes. Lumping the data for the two sexes, 17 animals were caught from age class zero and 44 animals from age class 10. Estimates of the survival rates from an initial run of the assessment model for the North Water population with an uniform age and sex structured catch, suggested that the number of animals in age class 10 is 33% of the number in age class zero. Hence, a c_0/c_{10} ratio of 0.13 can be expected for the North Water, and assumed here also for West and East Greenland.

Prior distributions

Prior probability distributions were assigned to adult survival (s_{ad}), juvenile survival (S_{juv}), the maximal birth rate (b_{max}), the age of reproductive maturity (a_m), the maximum sustainable yield level (msyl), the equilibrium abundance (N^*), and the catch history parameter (ϕ). Although the msyl is not an explicit parameter of the model, a uniform prior was assigned to it. This was possible since no prior distribution was assigned to the compensation parameter z ; given values for msyl and the other parameters of the model, a unique value is given for z . The fraction of females at birth (ϑ) was a fixed parameter across all model iterations.

The parameter ϕ sets a prior on the catch history, where the catch history that is applied in the parameterized iteration θ_i is given by a linear scaling between the low and the high catch histories, where the catch in year t of parameterization θ_i is

$$c_{t,i} = c_{l,t}(1 - \phi_i) + c_{h,t}\phi_i \quad (15)$$

where $c_{l,t}$ is the low and $c_{h,t}$ the high catch. The low catch history is thus applied when $\phi = 0$, and the high catch history when $\phi = 1$.

All the priors were uniform. The age of reproductive maturity was a discrete variable, while all other priors were continuous. The range of values for the priors (Table 5), together with the value for the fraction of females at birth, were based on various studies of walrus populations and previous modelling of walrus population dynamics (Fay, 1982; DeMaster, 1984; Fay *et al.*, 1989, 1997; Chivers, 1999). The annual natural survival rate of adults (s_{ad}) is unknown for walrus but was set in this study to range

between 0.90 and 0.98 with constant survival rate for all adult age classes. The juvenile annual survival rate (s_{juv}), that is also unknown, was set to 0.56–0.96. However, for each randomly selected parameter set, the upper bound on the juvenile survival rate was always set to be smaller than or equal to the randomly selected value for the adult survival rate.

The maximal birth rate (b_{max}), i.e., the maximal number of offspring per female per year, was set to range between 0.33 and 0.50 (Mansfield, 1958; Fay, 1982; Born, 2001), reflecting the assumption that each female produces one offspring every second or third year. The age of reproductive maturity (a_m) is set to 5–9 (Mansfield, 1958; Fay, 1982; Born, 2001), and the maximum sustainable yield level (msyl) to 0.50–0.80 (Eberhardt, 1992). The prior for the equilibrium abundance was set for each population separately with ranges wide enough to encompass plausible values given the estimates of current abundance.

The fraction of females at birth (ϑ) was set to the fixed value of 0.5 for all primary runs. However, an alternative run was performed for West Greenland walrus where ϑ was set to 0.60 (i.e., the fraction of females in the catch).

Realized priors, or post-model-pre-data probability distributions, were generated by discarding any parameterization θ_i that would not generate a viable model with a maximal population dynamic growth rate above zero. In result the discarded parameterizations were given zero likelihood, and the n_1 sampled parameterizations include only realistic models with positive maximal growth rates.

Results

Posterior distributions

The maximum importance weights relative to the total sum of importance weights for the 2 000 000 parameter sets were less than 0.0% for each of the five Bayesian runs. The number of unique parameter sets in the resample of 5000 parameter sets was above 4400 for all runs, and the maximum occurrences of a unique parameter set in the resample was no more than five (Table 6).

The median and 90% credibility intervals (CI) of the posterior parameter estimates are given in Table 7. As each model was fitted to only one abundance estimate there is hardly any information in the data to update the realized priors to new posterior estimates. This is exemplified for the West Greenland population (Figure 2), where nearly all

Table 5. The minimum and maximum values of the uniform priors used in the modelling of Greenland walrus populations s_{ad} is adult survival, s_{juv} juvenile survival, b_{max} the maximal birth rate, a_m the age of reproductive maturity of females, msyl the maximum sustainable yield level, ϕ the catch history parameter for scaling between the “low” and the “high” catch histories, and the equilibrium abundance for West Greenland (N^*_w), North Water (N^*_n), and East Greenland (N^*_e) walrus.

Parameter	s_{ad}	s_{juv}	b_{max}	a_m	msyl	ϕ	N^*_w	N^*_n	N^*_e
Minimum	0.90	0.56	0.33	5.00	0.50	0	3 000	2 000	200
Maximum	0.98	0.96	0.50	9.00	0.80	1	50 000	40 000	5 000

Table 6. The number of unique parameter sets in the resamples of 5000 parameter sets, and the maximum occurrence of a unique parameter set in the resample during modelling of three Greenland walrus populations.

Run	West ¹	West ²	West ³	North	East
Unique	4 683	4 539	4 446	4 782	4 992
Maximum	5	5	4	3	2

West = West Greenland; North = North Water; East = East Greenland. 1: $\theta = 0.5$, catches from 1900; 2: $\theta = 0.6$, catches from 1900; 3: $\theta = 0.5$, catches from 1820.

the posterior parameter estimates resemble the realized priors. The exception is the equilibrium abundance, where the posterior clearly differs from the realized prior, showing that the model is fitting to the abundance data by adjusting the equilibrium abundance.

Population dynamics

Assuming post 1999 catches equal to the catch in 1999, the following dynamics was obtained.

West Greenland

For walruses in West Greenland, the model based on the catches from 1900 suggested a population decline from an estimated equilibrium abundance of 16 300 (CI: 10 500–21 500; Table 7) individuals in 1900 to a projected extinction in 2000 (Figure 3 top). The yearly replacement yield had a maximum of 65 (CI: –10–142) individuals in 1934 (Figure 3 middle), while the replacement yield was estimated to be zero (CI: 0–0) in 2005. The annual birth rate reached a maximum of 0.41 calf per year after 1976 (Figure 3 bottom). Projection to extinction before 2010 was also the case with a female fraction at birth of 0.6, and for the model based on catches from 1820. In these cases the equilibrium abundance was estimated to be 13 900 (CI: 8330–18 600) and 16 800 (CI: 10 500–26 100) individuals, respectively (Table 7).

North Water

The model suggested that the North Water population declined almost linearly from an estimated equilibrium abundance of 15 100 (CI: 7800–22 300; Table 7) individuals in 1900, to a projected abundance of 349 (CI: 0–2230) individuals in 2010 (Figure 4 top). The population is predicted to be most severely depleted in 2010 with a depletion ratio of 0.02 (CI: 0.00–0.21), while the depletion ratio in 2005 was estimated to be 0.07 (CI: 0.01–0.24). The yearly replacement yield had a maximum of 119 (CI: 23–196) individuals in 1948, while the yield in 2005 was estimated to be 11 (CI: –4–92) (Figure 4 middle). The annual birth rate grew steadily to a maximum of 0.41 (CI: 0.34–0.49) calf per year at the end of the projection period (Figure 4 bottom).

Table 7. Parameter estimates given by the median and the 90% credibility intervals of the posterior distribution. z is the compensation parameter, m_{sy} the maximum sustainable yield rate, and the other parameters are explained in Table 2.

Parameter	S_{ad}	S_{juv}	b_{max}	a_m	m_{sy}	m_{sy}	z	ϕ	N^*									
West ¹	0.95	0.98	0.76	0.92	0.41	0.49	7	9	0.02	0.07	0.61	0.74	2.67	7.10	0.51	0.95	16 300	21 500
		0.91	0.58	0.58	0.34	0.34	5	5	0.00	0.00	0.51	0.51	1.11	1.11	0.05	0.05	10 500	10 500
West ²	0.94	0.97	0.75	0.92	0.41	0.49	7	9	0.02	0.07	0.62	0.74	2.82	7.13	0.50	0.95	13 900	18 600
		0.91	0.58	0.58	0.34	0.34	5	5	0.00	0.00	0.51	0.51	1.11	1.11	0.05	0.05	8 330	8 330
West ³	0.95	0.98	0.76	0.92	0.42	0.49	7	9	0.02	0.07	0.62	0.74	2.74	7.13	0.51	0.95	16 800	26 100
		0.91	0.58	0.58	0.34	0.34	5	5	0.00	0.00	0.51	0.51	1.12	1.12	0.05	0.05	10 500	10 500
North	0.95	0.97	0.78	0.93	0.42	0.49	7	9	0.02	0.07	0.62	0.74	2.70	7.10	0.49	0.95	15 100	22 300
		0.91	0.59	0.59	0.34	0.34	5	5	0.00	0.00	0.51	0.51	1.11	1.11	0.05	0.05	7 800	7 800
East	0.96	0.98	0.81	0.94	0.42	0.49	7	9	0.04	0.10	0.63	0.75	2.88	7.23	0.46	0.94	1 610	2 860
		0.92	0.60	0.60	0.34	0.34	5	5	0.00	0.00	0.51	0.51	1.12	1.12	0.04	0.04	941	941

West = West Greenland; North = North Water; East = East Greenland. 1: $\theta = 0.5$, catches from 1900; 2: $\theta = 0.6$, catches from 1900; 3: $\theta = 0.5$, catches from 1820.

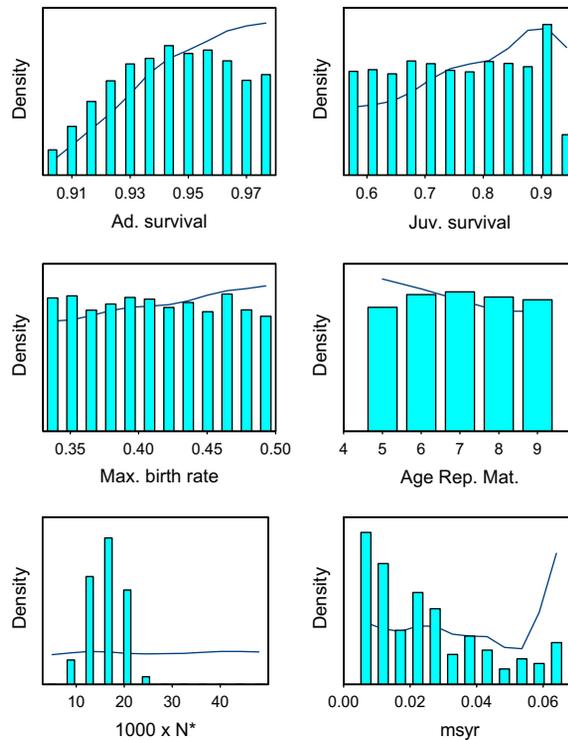


Figure 2. Realized priors (curves) and the posterior distributions (bars) for six parameters for the West Greenland population of walrus ($\theta = 0.5$, catches from 1900). The parameters are annual adult survival, annual juvenile survival, the maximal birth rate (calf per female per year), the age of reproductive maturity (years), the equilibrium abundance, and the msyr.

East Greenland

The model indicated that the East Greenland walrus population declined from an equilibrium abundance of 1610 (CI: 941–2860; Table 7) individuals in 1889 and reached a maximal depletion of 0.60 (CI: 0.34–0.95) in 1933. The population then increased steadily to an estimated abundance of 1310 (CI: 808–2200) in 2010 (Figure 5 top). The projected abundance in 2005 is close to the equilibrium, with an estimated depletion ratio of 0.97 (CI: 0.38–1.00). The yearly replacement yield had a maximum of 28 (CI: –16–93) individuals in 1889, while the yield in 2005 was estimated to 10 (CI: 8–19) (Figure 5 middle). The annual birth rate had a maximum of 0.34 (CI: 0.19–0.47) calf per year in 1933 (Figure 5 bottom).

Meeting management objectives

Only in the case of the East Greenland walrus population could the management criteria applied in this study be met (Figure 6). For this population the probability of meeting the management objectives was 0.93 with future total removals (i.e., catch and loss) similar to the current removal of 10 individuals per year, and the probability was 0.84 and 0.78 for a future annual removal of 15 and 18 individuals, respectively. For the North Water population, where the

annual total removal from 1990 to 1999 varied between 123 and 381 individuals (average = 208 walrus per year), the probability of meeting the management objectives was larger than 0.50 only for total removals below 22 individuals per year. The probability was 0.85 for an annual removal of nine individuals, 0.91 for an annual removal of seven individuals, and 0.95 for an annual removal of five individuals. For the West Greenland population, given a female fraction at birth of 0.50, the probability of meeting the management objectives was below 0.01, even with the removal of only a single individual. The reason that the management objectives could not be fulfilled even with no catch was because the population was predicted to become extinct. And with a female fraction at birth of 0.60, the probability of meeting the management objectives with the harvest of a single individual was only 0.03.

Discussion

The model

Previous attempts to simulate walrus population dynamics have used discrete models with density regulations for modelling hypothetical populations (DeMaster, 1984; Chivers, 1999). Chivers (1999) applied an individual,

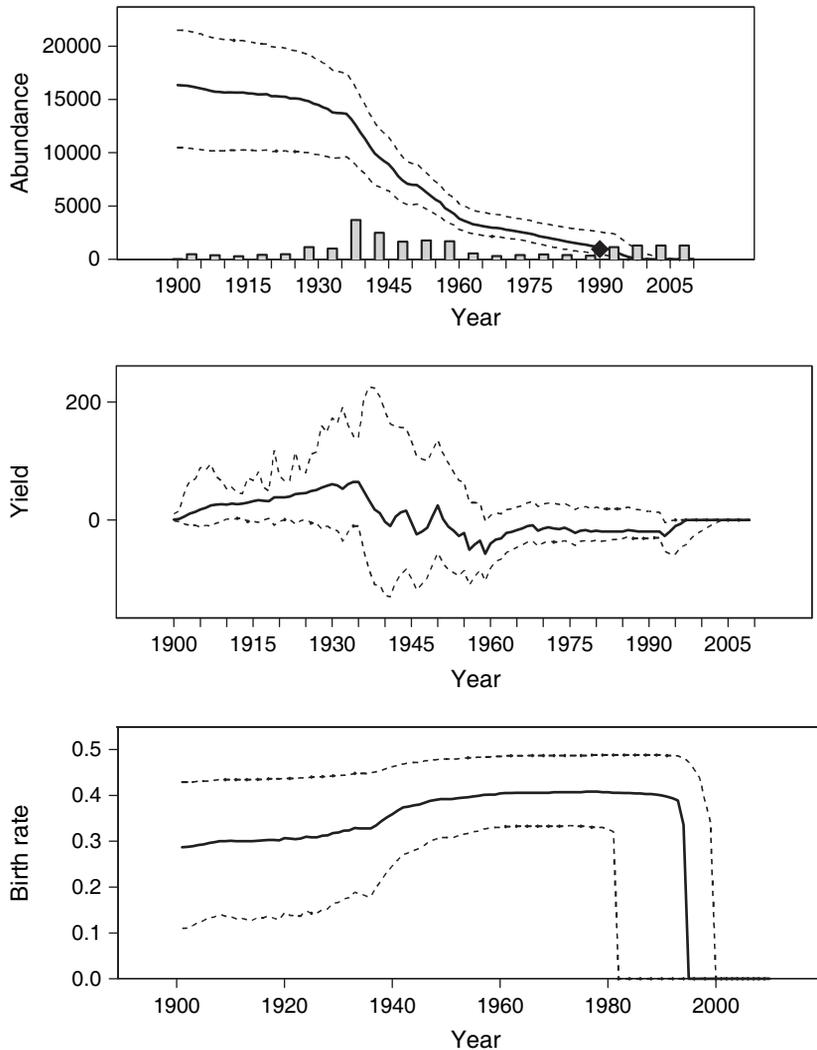


Figure 3. Projections of the median and the 90% credibility intervals of the total abundance (top), the annual replacement yield (middle), and the annual birth rate (bottom) for the West Greenland walrus population, 1900–2010. The low catch history (Table 1) is shown in five-year intervals by the bars in the top figure, with the yearly catches after 1999 being set to the catches in 1999. The diamond is the abundance estimate.

age-based population model with density-dependent changes in rates of juvenile survival, birth, and maturation. This model also differed from previous modelling efforts for walrus populations by incorporating senescence in the survival rates and by making calf survival dependent on the survival of its mother.

Born *et al.* (1997) and Gjertz *et al.* (1998) used a simple recursive relationship to back-calculate the size of the East Greenland and Franz Josef Land walrus populations, respectively. This method used estimates of current population size, total removals, and fixed values for maximum net recruitment rate. We extended this calculation to include also West Greenland and North Water walruses, and we made the simulation more realistic by incorporating both

age and sex structure as well as density regulation in the birth rate. Like Chivers (1999), we made calf survival during the first year depend on the survival of the mother, although this was done at the population level. We did not elaborate an individual-based model, because this adds much complexity to the model, while only providing a marginal advantage unless the population is so small that the effects of demographic stochasticity are strong. This is unlikely for populations above a few hundred individuals (Lande *et al.*, 2003).

Although the priors of the model were initially drawn from uniform distributions, an approximately uniform realized prior was found only for equilibrium abundance, while the other parameters showed realized priors that

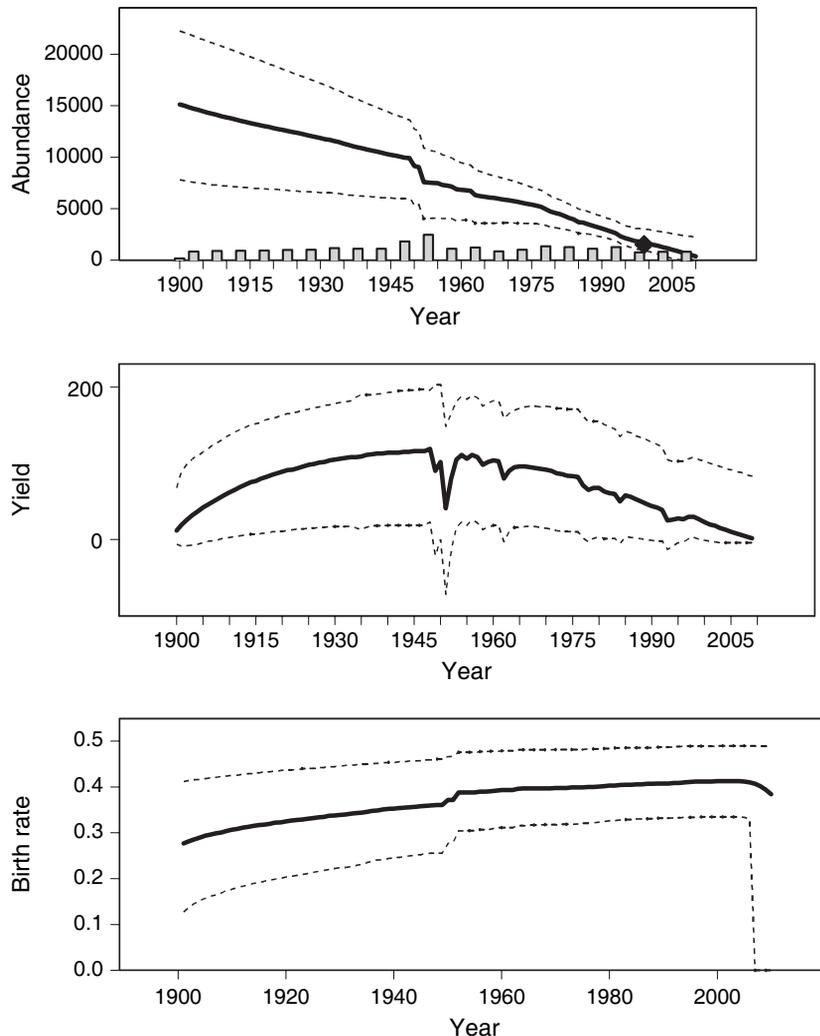


Figure 4. Projections of the median and the 90% credibility intervals of the total abundance (top), the annual replacement yield (middle), and the annual birth rate (bottom) for the North Water walrus population, 1900–2010. The low catch history (Table 6) is shown in five-year intervals by the bars in the top figure, with the yearly catches after 1999 being set to the catches in 1999. The diamond is the abundance estimate.

clearly differed from uniform. The reason is the model constraint of a positive maximal growth rate that limited the set of possible parameter combinations. Combinations of low survival, low maximal birth rate, and a high age of reproductive maturity are generally in conflict with a positive maximal growth rate.

Biological parameters

The ranges chosen by us for the various prior distributions were based on previous knowledge of the biology of Atlantic and Pacific walrus and estimates of their vital parameters. Although recognized as two geographically and taxonomically distinct subspecies (e.g., Fay, 1985), the life history of Atlantic and Pacific walrus appears to be very

similar. However, in both cases the segregation of different sex and age classes for most of the year, and the selective hunting pattern make it difficult to obtain unbiased samples for determining biological parameters (Fedoseev and Goltsev, 1969; Fay, 1982; DeMaster, 1984). The posterior estimates of the biological parameters were generally in good agreement with estimates in other studies, even though the data signal of the single abundance estimates for the three walrus populations was not sufficiently strong to update the realized priors to new posterior estimates (Figure 2). These values are discussed in detail below.

The sex ratio in walrus populations is not well known. On the assumption that walruses are polygynous, an adult sex ratio of one male to three females has been suggested in the population of Pacific walrus (Fay, 1982; Fay *et al.*,

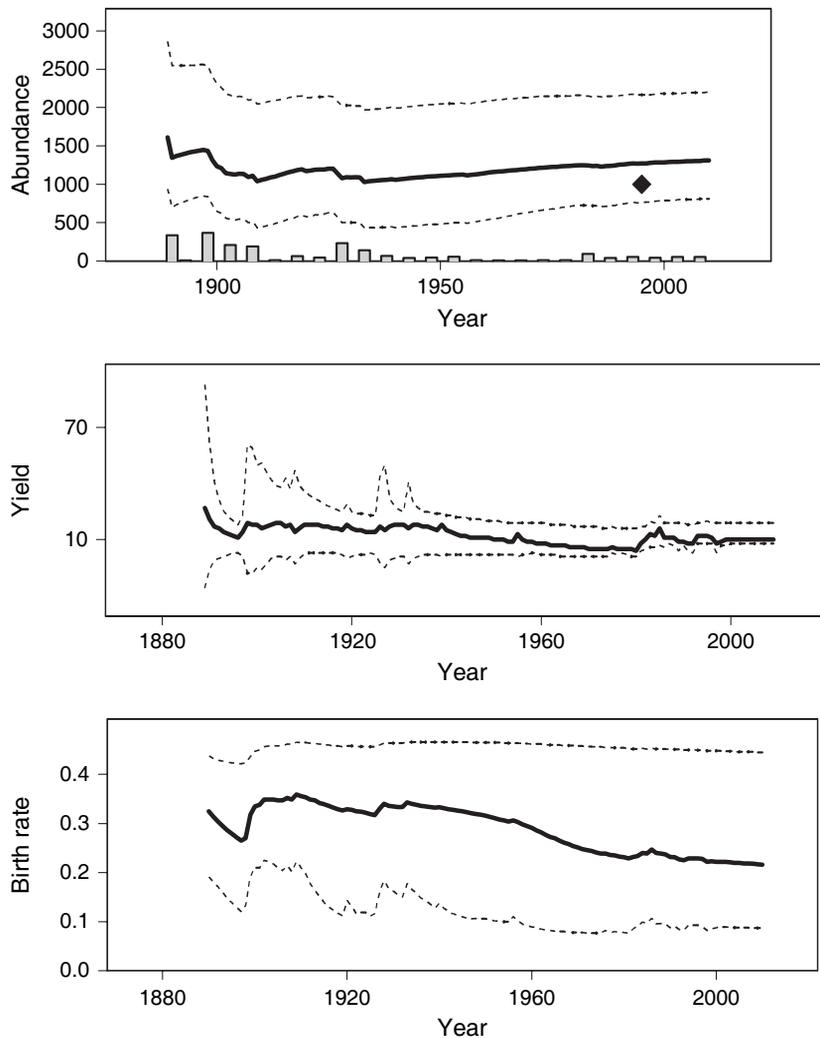


Figure 5. Projections of the median and the 90% credibility intervals of the total abundance (top), the annual replacement yield (middle), and the annual birth rate (bottom) for the East Greenland walrus population, 1889–2010. The low catch history (Table 7) is shown in five-year intervals by the bars in the top figure, with the yearly catches after 1999 being set to the catches in 1999. The diamond is the abundance estimate.

1984; Sease and Chapman, 1988). DeMaster (1984) adopted this sex ratio in his modelling of the dynamics of a hypothetical walrus population. The sex ratio in the Pacific walrus changed from (M:F) 1:1.7 to 1:3 between 1960 and 1985 during a period of population increase according to Fay *et al.* (1997), a pattern that is actually expected from density and frequency dependent natural selection (Witting, 1997, 2000).

To our knowledge there are no indications of the sex ratio being severely skewed towards females in Atlantic walrus sub-populations, and we therefore assumed that it was even in the evaluation of the Greenland situation. An exception was West Greenland, where we also made a simulation of the population dynamics assuming a surplus of females (based on small recent sample of the catch and

historical information). Although the female biased version of the model estimated a population that was slightly better in sustaining the historical harvest, the change in sex ratio was not sufficient to avoid a prediction of the extirpation of the population in 2010.

In Pacific walrus total annual mortality for adult males has been estimated at 8–13% (Burns, 1965; Fedoseev and Goltsev, 1969). DeMaster (1984) suggested an annual mortality of about 9% for adult males and considered it likely that total annual mortality of adult females was much lower.

The natural mortality rate in walrus is not well established but is assumed to be low because productivity is low and longevity is relatively high (Fay, 1982; Fay *et al.*, 1997). Natural mortality rate has been estimated to be

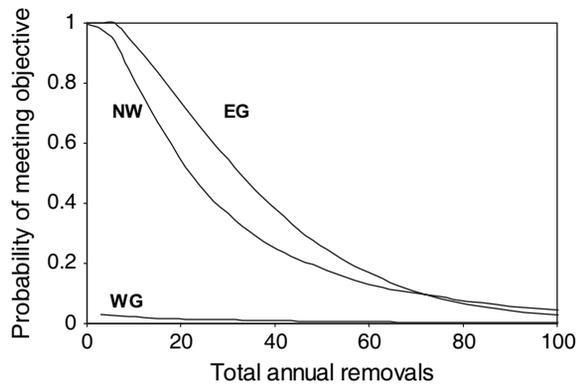


Figure 6. The probability of meeting the management objectives for annual total removals of between 0 and 100 walrus in the period 2005–2010. (EG) The East Greenland population, (NW) the North Water population, (WG) the West Greenland population assuming a female fraction at birth of 0.6.

3% to 5% for the entire population of Pacific walrus (DeMaster, 1984; Fay *et al.*, 1989). Fay *et al.* (1994) suggested that natural mortality in adults was higher than 1%, but probably not higher than 2% per year. A natural mortality rate of 1.5% per year was applied in simulations of Bering Sea walrus (Fay *et al.*, 1997). Chivers (1999) used an estimate of survival in adults between 9 and 24 years to 0.98 (it then decreased until 40 years of age).

Survival in calves until their second year of life (during this year suckling ceases) has been estimated to range between 0.5 and 0.9 (Chivers, 1999, and references therein). A survival rate in calves up to two years of age of 0.66 to 0.88 was used by Chivers (1999) for simulations of walrus population dynamics.

We used 0.90 to 0.98 for the prior for annual adult survival rate (i.e., annual natural mortality: 2% to 10%), and 0.56 to 0.96 in calves. The resulting estimate of survival obtained by the posterior median was 0.94 (West Greenland) to 0.96 (East Greenland) in adults, and 0.75 (West Greenland) to 0.81 (East Greenland) in calves.

Our prior of maximum annual fecundity ranged between 0.33 and 0.5 cal per mature female per year, with the posterior median being 0.41 or 0.42 for the different model runs. Based on analyses of reproductive organs, rates of fecundity have been estimated at between 0.29 and 0.40 in walrus (Mansfield, 1958; Fay, 1982; Garlich-Miller and Stewart, 1999; Born, 2001). According to Mansfield (1958), the reproductive cycle of the female Atlantic walrus in Foxe Basin was basically biennial, but, to an unknown extent, older females may give birth at three- or four-year intervals. According to Fay (1982), female Pacific walrus tend to breed at two-year intervals or less often, and hence maximum fecundity was thought to be 0.5 (Fay *et al.*, 1997).

The priors for age at maturity (i.e., first birth) ranged between five and nine years of age, and the posterior median was seven years for all populations. Mansfield

(1958) found that the age at first ovulation varied from 5 to 10 years, but that the majority of females in his Canadian sample became sexually mature at the age of seven. Born (2001) found that the average age at sexual maturity was six years in Atlantic walrus from the North Water and stated that attainment of sexual maturity in female Atlantic walrus is similar to that in the Pacific subspecies. By the age of six years, two-thirds of the female Pacific walrus have ovulated at least once, and by the 8th or 9th year practically all have ovulated (Fay, 1982).

Our fixed parameter for sex ratio at birth (1:1) was in accordance with findings in Atlantic walrus from the North Water (Born, 2001) and in Pacific walrus from the Bering Strait region (Fay, 1982; Fay *et al.*, 1984).

In most populations of large marine mammals, msyl is thought to be within the (0.50; 0.80) range chosen for the prior distributions in this paper (Anon., 1986; Eberhardt, 1992). The median posterior estimate of msyl was almost identical at 0.62 (CI: 0.51–0.74) for all Greenland populations.

The population birth rate (fraction of neonates in the total population) has been estimated at 0.07 (Mansfield, 1966) or 0.11 (Mansfield, 1973) in Atlantic walrus and between 0.12 and 0.17 in Pacific walrus (Fedoseev and Goltsev, 1969; Fay, 1982). Instantaneous net growth rate of the population of Pacific walrus during the late 1950s to mid-1970s was estimated at 0.067 (Tavrovski, 1971; Sease and Chapman, 1988), indicating a finite growth rate of about 7% per year for a population in a phase of growth under favourable environmental conditions with no food limitations. Chivers (1999) modelled an annual maximum growth rate of 8% but stressed that because survival rates are unknown for walrus, the models growth rate should not be considered an estimate of maximum growth rate for walrus.

DeMaster (1984) estimated that the maximum sustainable yield of adult females (four years and older) would be 5.1% of the total population of females. He suggested that

an adult female harvest of 1% to 5% could be sustained. Fay (1985) suggested that an annual hunting mortality of 5% to 7% of the total population of walrus would be sustainable. Gjertz *et al.* (1998) suggested a net maximum recruitment rate of 5% to be the most plausible and in compliance with the estimates of current abundance of walrus at Franz Josef Land. Assuming an even sex ratio, our estimate of m_{sy} for the mature component of the population was 0.02 (CI: 0.00–0.07) for the West Greenland and North Water walrus populations, and 0.04 (CI: 0.00–0.10) for the East Greenland population.

Abundance and population identity

Inevitably our modelling exercise was influenced by the uncertainties about current abundance, delineation of populations (in particular in West Greenland), and total removal.

The surveys for determination of abundance in western Greenland were conducted in 1990 and 1991 during late March and early April. The majority of walrus observed were hauled out on the ice. Walrus tend to haul-out during relatively warm and calm days (Fay and Ray, 1968), and they are generally difficult to detect in the water (Estes and Gilbert, 1978; Born *et al.*, 1994), partially due to their cryptic colour. Likely, an unknown number of walrus was missed by the observers in West Greenland. Hence, we expect that these estimates of abundance were not corrected for observer bias or missed observations (Born *et al.*, 1994) and it cannot be precluded that particularly walrus in water were missed. Hence, we suspect that the estimates of abundance were negatively biased (i.e., minimum estimates). This is also suggested by our analysis which, based upon the abundance estimate, predicts population extirpation before 2000, while walrus are still being caught in West Greenland.

For the purpose of the present study we applied a correction factor to include walrus that were submerged during the surveys. The general correction factor (surface:subsurface ratio of 1:4) used here is consistent with most observations of feeding walrus (Fay, 1982; Wiig *et al.*, 1993; Born and Knutsen, 1997; Born *et al.*, 2003). Most of these observations have been made during summer when walrus feed intensively. Walrus feed in western Greenland (Born *et al.*, 1994) but information on surface:subsurface ratios in walrus during March–April, when the surveys were flown, are not available. However, an adult male walrus equipped with a satellite-transmitter in Northeast Greenland (2000/2001) spent an average of 19.3% of its time in the upper 2 m of the water column in December–January (16.3% and 23.1%, respectively) (Born, unpublished data). This supports the notion that walrus generally dive in a highly stereotypic manner, and also that the correction factor used by us is appropriate.

Irrespective of general uncertainties associated with abundance estimates obtained from aerial surveys of walrus, not only in West Greenland but also in other

studies (cf. Gilbert, 1989; Udevitz *et al.*, 2001), we believe that the estimate used in the present study for the total group of walrus wintering in West Greenland is in the right order of magnitude.

It was attempted to enumerate the North Water population during five days in August 1999 when the coasts of eastern Ellesmere Island (north to Flaggler Bay), Jones Sound, Cornwallis and Bathurst Islands, and Grinnell Peninsula were surveyed by helicopter and ground counts (DFO and GINR, unpublished data; Dunn, 2000). The surveys covered all areas where walrus from the North Water population are known to haul-out on land during summer (Born *et al.*, 1995). However, the number of walrus hauling out on land on any given day may fluctuate (Hills, 1992; Born and Knutsen, 1997) making any short-period census sensitive to daily fluctuations in numbers. Furthermore, walrus can move up to 100 km from their terrestrial haul-outs to feed (e.g., Born and Knutsen, 1992, 1997; Born and Acquarone, 2005) meaning that surveys that follow coastlines may miss an unknown proportion of walrus at sea. We applied general correction factors to include the fraction of walrus not present at the haul-out and/or submerged. By more or less arbitrarily adding another 500 to account for walrus in unsurveyed areas we derived an estimate of the total population of 1500. Based on miscellaneous ground counts and aerial surveys since 1976, Born *et al.* (1995) suggested that the North Water population of walrus numbers approximately 1700–2000 and perhaps as many as 3000. Given the uncertainties about the fraction present at the haul-out during the surveys, and the fact that walrus far out at sea inevitably were missed, we cannot exclude the possibility that the estimate of abundance of the North Water population used in this study is negatively biased.

The estimate of abundance in East Greenland was based on Born *et al.* (1997) who derived at a rough estimate of 500–1000 walrus from miscellaneous ground and aerial counts north of approximately 74°N. They argued that the highest bound of this estimate was the most likely (Born *et al.*, 1997).

Born *et al.* (1997) used a simple recursive relationship to back-calculate the size of the East Greenland walrus population, using an estimate of current population size of 500–1000. Their estimates of the population size in 1889 ranged between 676 and 1934 walrus for different combinations of parameters (Born *et al.*, 1997). The estimate in the present study of the equilibrium abundance in 1889 was 1610 (95% CI: 941–2860).

The results in the present study are influenced by assumptions about whether the populations considered represent separate demographic units or not. We assumed that they did.

Information on distribution and occurrence indicates that when walrus were more abundant in the Baffin Bay area during the beginning of the 20th century, walrus in this

region (including the West Greenland and North Water animals) were part of one large population (Born *et al.*, 1995, and references therein). However, recent data on migration and distribution (Born *et al.*, 1994, 1995) and genetic analyses (Andersen and Born, 2000) indicate that there is very limited exchange between walruses in West Greenland and in the North Water area.

A comparison of walruses from the Hudson Strait-eastern Hudson Bay region indicated that they differ genetically from those in West Greenland (Andersen and Born, unpublished data). Furthermore, walruses from West Greenland differed in lead isotope ratios from walruses in these two areas (Outridge *et al.*, 2003). However, the absence of walruses from West Greenland during summer and scattered observations of walruses in Davis Strait midway between Southeast Baffin Island and Central West Greenland (Born *et al.*, 1994) indicate a connection between walruses in those two areas. In that case the group of walruses that winters in West Greenland represents a part of a population which ranges over eastern Baffin Island but for which numbers are unknown (Born *et al.*, 1995).

The study of regional variation in lead isotope ratios in walruses indicated a sub-structuring and subdivision in some of the populations identified from distribution and genetics (Outridge *et al.*, 2003). For example, walruses that winter in West Greenland and summer at SE Baffin Island may mix with but not mate with walruses occurring in Baffin Island year-round. The breeding season of Atlantic walruses is March–April (Born, 2001, 2003) when walruses are found in West Greenland.

Walruses are caught by the Inuit at southeastern Baffin Island (Born *et al.*, 1995; NAMMCO, 1995). Therefore West Greenland walruses may be subject to hunting while summering there. However, owing to lack of specific information on hunting practices in Baffin Island, we did not include catches from there in our simulations of the West Greenland population.

Despite uncertainties about the delineation of the West Greenland population, we decided to take a precautionary approach by treating it as a separate population unit.

Information on distribution (Born *et al.*, 1995) and genetic (Andersen and Born, 2000) and isotopic variation (Outridge *et al.*, 2003) indicates that the North Water population constitutes a separate demographic unit. However, some fine-scale sub-structuring of the population was indicated (Andersen and Born, 2000; Outridge *et al.*, 2003).

Similar information indicates that the East Greenland population is a distinct population with little exchange with the neighbouring groups (Born *et al.*, 1997; Andersen *et al.*, 1998; Born *et al.*, 2001).

Removals

The modelling was influenced by the fact that catch data were insufficient for several years and periods. Furthermore, losses were estimated in most cases.

Catches from the West Greenland population were reported for most years since 1900. However, the system of reporting until 1987, based on Hunters Lists of Game, was inadequate. The new system of reporting (“Piniarneq”) that started in 1993 also suffers from uncertainties about the actual takes (for a description of the Greenland catch reporting systems, see Born *et al.* (1994); Kapel and Rosing-Asvid (1996); Teilmann and Kapel (1998)). In particular the sudden fourfold increase in reported catch for West Greenland from 1993 and onwards is critical for our assessment. Furthermore, for years with no reporting we had to estimate the catch. This was particularly the case for the North Water population.

Until about 1910, Scottish whalers caught walruses in the Baffin Bay region including in West Greenland and the North Water areas (Ross and MacIver, 1982). Norwegian sealers and whalers took walruses between ca. 1910 and 1923 offshore in West Greenland, and made large catches around the 1950s presumably in northern Baffin Bay (Born *et al.*, 1995, and references therein). For all three walrus populations great uncertainty exists about the numbers taken by European whalers and sealers. Furthermore, there are uncertainties about location and numbers in the original sources. A general lack of information about the catch of walrus by foreigners precluded us from pursuing this matter further. For this reason, the catches used in the present study are negatively biased to an unknown extent. However, in West Greenland we attempted to estimate the catches also by foreigners back to 1820. However, doing so did not alter the conclusions about the pristine population and current status.

The catch of walruses in East Greenland by foreigner sealers was intense during the last decade of the 19th century and the first decades of the 20th century (Born *et al.*, 1997). Those researchers extracted information on catches from published and unpublished sources. However, because information in many cases was insufficient on numbers of vessels participating in the hunt and number of walrus taken historical catches were underestimated. For the same reason the equilibrium population (i.e., pristine population) may have been underestimated in the present paper.

We tried to incorporate the uncertainty in the catch histories into the analysis by applying a uniform prior scaling between a low and a high catch history. Irrespective of the catch history assumed, the main results of the simulation basically remained the same.

Conclusions

The Bayesian approach to modelling walrus populations proved valuable in this study because in the existence of non-ideal data it allowed us (i) to simulate the historical development and current status of the three walrus populations in Greenland, and (ii) to quantify the trade-off

between the uncertainties inherent in data and the probability of meeting the management objectives. Owing to the lack of specific management objectives for the exploitation of walrus in Greenland, we used management objectives defined by IWC for the sustainable management of aboriginal exploitation of large whales.

The study indicated that the West Greenland population was heavily exploited during the last century and that the current abundance is at best only a few per cent of the historical abundance. The population is still being exploited far above a sustainable level. Further, the North Water population has been subject to intense hunting during the same period, where it has declined to a current depletion of less than 10% of the 1900 level. The current removal is apparently unsustainable, with a drastic reduction in the removal required if this population should increase again. Finally, the East Greenland population was heavily exploited late in the 19th century and in the first half of the 20th century, where it was depleted to approximately 50% in 1933. The abundance has since increased to a current level close to the abundance in 1889, with the current catch being sustainable.

These conclusions suffer from a lack of adequate information on population size, delineation of populations, and catch and losses. Future research must aim at providing information on in particular (i) the delineation of the walrus population that is exploited in West Greenland, (ii) abundance of all three Greenland walrus populations, and (iii) catch levels and site and method specific losses.

Acknowledgements

We thank Michael Kingsley (Greenland Institute of Natural Resources), Carryn Cunningham (University of Cape Town), Østein Wiig (University of Oslo), and an anonymous reviewer for many helpful comments.

References

- Alvarez-Flores, C. M., and Heide-Jørgensen, M. P. 2004. A risk assessment of the sustainability of the harvest of beluga, *Delphinapterus leucas* (Pallas 1776), in West Greenland. *ICES Journal of Marine Science*, 61: 274–286.
- Andersen, L. W., and Born, E. W. 2000. Identifications of two genetically different sub-populations of Atlantic walrus (*Odobenus rosmarus rosmarus*) in West and Northwest Greenland. *Canadian Journal of Zoology*, 78: 1999–2009.
- Andersen, L. W., Born, E. W., Gjertz, I., Wiig, Ø, Holm, L., and Bendixen, C. 1998. Population structure and gene flow of the Atlantic walrus (*Odobenus rosmarus rosmarus*) in the eastern Atlantic Arctic based on mitochondrial DNA and microsatellite variation. *Molecular Ecology*, 7: 1323–1336.
- Anonymous. 1986. Annex F. Report on the Sub-Committee on Northern Hemisphere Minke Whales. Report of the International Whaling Commission, 36: 79–85.
- Berger, J. O. 1985. *Statistical Decision Theory and Bayesian Analysis*, 2nd ed. Springer-Verlag, New York.
- Born, E. W. 2001. Reproduction in female Atlantic walrus (*Odobenus rosmarus rosmarus*) from north-western Greenland. *Journal of Zoology (London)*, 255: 165–174.
- Born, E. W. 2003. Reproduction in male Atlantic walrus (*Odobenus rosmarus rosmarus*) from the North Water (N Baffin Bay). *Marine Mammal Science*, 19: 819–831.
- Born, E. W., and Acquarone, M. 2005. An estimation of walrus (*Odobenus rosmarus*) predation on bivalves in the Young Sound area (NE Greenland). In *Carbon Cycling in Arctic Marine Ecosystems: Case Study – Young Sound*. Ed. by S. Rysgaard, and R. N. Glud. Meddelelser om Grønland, Bioscience, Special Issue. Copenhagen, Denmark.
- Born, E. W., Andersen, L. W., Gjertz, I., and Wiig, Ø 2001. A review of genetic relationships of Atlantic walrus (*Odobenus rosmarus rosmarus*) east and west of Greenland. *Polar Biology*, 24: 713–718.
- Born, E. W., Dietz, R., Heide-Jørgensen, M., and Knutsen, L. 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., Gjertz, I., and Reeves, R. 1995. Population assessment of Atlantic walrus. *Norsk Polarinstitutt Meddelelser*, 138: 1–100.
- Born, E. W., Heide-Jørgensen, M., and Davis, R. 1994. The Atlantic walrus (*Odobenus rosmarus rosmarus*) in West Greenland. *Meddelelser om Grønland, Bioscience*, 40: 1–33.
- Born, E. W., and Knutsen, L. Ø. 1992. Satellite-linked radio tracking of Atlantic walrus (*Odobenus rosmarus rosmarus* L.) in northeastern Greenland, 1989–1991. *Zeitschrift für Säugetierkunde*, 57: 275–287.
- Born, E. W., and Knutsen, L. Ø. 1997. Haul-out activity of male Atlantic walrus (*Odobenus rosmarus rosmarus*) in northeastern Greenland. *Journal of Zoology (London)*, 243: 381–396.
- Born, E. W., Rysgaard, S., Ehlme, G., Sejr, M., Acquarone, M., and Levermann, N. 2003. Underwater observations of foraging free-living walrus (*Odobenus rosmarus*) including estimates of their food consumption. *Polar Biology*, 26: 348–357.
- Bruemmer, F. 1971. Notes on the sea mammals in Thule district, Greenland. Unpublished manuscript, 29 pp., Montreal, Canada. Available at Greenland Institute of Natural Resources, P.O. Box 570, DK-Nuuk, Greenland.
- Buckland, S. T. 1992. Proposal for standard presentation of abundance estimates. Report of the International Whaling Commission, 42: 235.
- Burns, J. 1965. The walrus in Alaska, its ecology and management. Unpublished manuscript, 45 pp., Alaska Department of Fish and Game, Juneau, USA. Available at Greenland Institute of Natural Resources, P.O. Box 570, DK-Nuuk, Greenland.
- Chapskii, K. 1936. The walrus of the Kara Sea. In *Biology*, pp. 1–114. Ed. by N. A. Smirnov. Transactions of the Arctic Institute. vol. LXVII: Great Northern Sea Route, Leningrad, Russia. Translated by F. H. Fay & B. A. Fay.
- Chivers, S. 1999. Biological indices for monitoring population status of walrus evaluated with an individual-based model. In *Marine Mammal Survey and Assessment Methods*, pp. 239–247. Ed. by G. W. Garner, S. C. Amstrup, J. L. Laake, B. F. L. Manly, L. L. McDonald, and D. G. Robertson. Proceedings of the Symposium on Surveys, Status & Trends of Marine Mammal Populations. Seattle, Washington, USA, 25–27 February 1998. Balkema, A.A., Rotterdam, Brookfield, The Netherlands.
- De la Mare, W. K. 1986. Fitting population models to time series of abundance data. Report of the International Whaling Commission, 36: 399–418.
- DeMaster, D. 1984. An analysis of a hypothetical population of walrus. In *Soviet-American Cooperative Research on Marine Mammals*, pp. 77–80. Ed. by F. H. Fay, and G. A. Fedoseev. Pinnipeds, vol. 1: National Oceanographic Atmospheric Administration Technical Report NMFS 12, Washington, DC, USA.

- Dunn, J. 2000. Walrus aerial survey report. Unpubl. report to Department of Fisheries and Oceans, Winnipeg, and Greenland Institute of Natural Resources, Nuuk, 1–7.
- Eberhardt, L. 1992. An analyses of procedures for implementing the dynamic response method. *Marine Mammal Science*, 8: 201–212.
- Estes, J., and Gilbert, J. 1978. Evaluation of an aerial survey of Pacific walruses (*Odobenus rosmarus divergens*). *Journal of Fisheries Research Board of Canada*, 35: 1130–1140.
- Fay, F. 1982. Ecology and Biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North American Fauna U.S. Department of the Interior Fish and Wildlife Service, 74: 1–279.
- Fay, F. 1985. *Odobenus rosmarus*. Mammalian species. *American Society of Mammalogists*, 238: 1–7.
- Fay, F., Burns, J., Stoker, S., and Grundy, J. 1994. The struck-and-lost factor in Alaskan walrus harvests, 1952–1972. *Arctic*, 47: 368–373.
- Fay, F., Eberhardt, L., Kelly, B., Burns, J., and Quakenbush, L. 1997. Status of the Pacific walrus population, 1950–1989. *Marine Mammal Science*, 13: 537–565.
- Fay, F., Kelly, B., and Sease, J. 1989. Managing the exploitation of Pacific walruses: a tragedy of delayed response and poor communication. *Marine Mammal Science*, 5: 1–16.
- Fay, F., and Ray, C. 1968. Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). I. Evidence from thermoregulatory behavior. *Zoologica*, 53: 1–18.
- Fay, F., Ray, G., and Kibalchich, A. 1984. Time and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. In *Soviet-American Cooperative Research on Marine Mammals*, pp. 81–88. Ed. by F. H. Fay, and G. A. Fedoseev. Pinnipeds, vol. 1: National Oceanographic Atmospheric Administration Technical Report NMFS 12, Washington, DC, USA
- Fedoseev, G., and Goltsev, V. 1969. Age-sex structure and reproductive capacity of the Pacific walrus population. *Zoologicheskij Zhurnal*, 48: 407–413.
- Garlich-Miller, J. L., and Stewart, R. E. A. 1999. Female reproductive patterns and foetal growth of Atlantic walruses (*Odobenus rosmarus rosmarus*) in Foxe Basin, Northwest Territories, Canada. *Marine Mammal Science*, 15: 179–191.
- Gilberg, R. 1976. The Polar Eskimo population, Thule district, North Greenland. *Meddelelser om Grønland*, 203: 1–87.
- Gilbert, J. 1989. Aerial census of Pacific walruses in the Chukchi Sea, 1985. *Marine Mammal Science*, 5: 17–28.
- Givens, G. H., Zeh, J. E., and Raftery, A. E. 1995. Assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales using the BALEEN II model in a Bayesian synthesis framework. Report of the International Whaling Commission, 45: 345–364.
- Gjertz, I., Wiig, Ø., and Øritsland, N. 1998. Backcalculation of original population size for walruses *Odobenus rosmarus* in Franz Josef Land. *Wildlife Biology*, 4: 223–230.
- Hills, S. 1992. The effect of spatial and temporal variability on population assessment of Pacific walruses. Ph.D. dissertation, University of Maine, Orono, Maine, USA.
- Innes, S., and Stewart, R. E. A. 2002. Population size and yield of Baffin Bay beluga (*Delphinapterus leucas*) stocks. NAMMCO Scientific Publications, 4: 225–238.
- IWC International Whaling Commission, 2000. International Convention for the Regulation of Whaling, 1946. Schedule. Annual Report of the International Whaling Commission 1999, 77–90.
- Kapel, F., and Rosing-Asvid, A. 1996. Seal hunting statistics for Greenland 1993 and 1994 according to a new system of collecting information, compared to previous Lists-of-Game. NAFO Scientific Council Studies, 26: 71–86.
- Lande, R., Engen, S., and Sæther, B. 2003. *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford.
- Mansfield, A. 1958. The biology of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus) in eastern Canada. Fisheries Research Board of Canada Manuscript Report Series (Biology), 653: 1–146.
- Mansfield, A. 1966. The walrus in Canada's Arctic. *Canadian Geographic Journal*, 72: 88–95.
- Mansfield, A. 1973. The Atlantic walrus *Odobenus rosmarus divergens* in Canada and Greenland. In *Seals. Proceedings of a Working Meeting of Seal Specialists on Threatened and Depleted Seals of the World*, held under the auspices of the Survival Service Commission of IUCN (International Union for Conservation of Nature and Natural Resources), 18–19 August 1972 at the University of Guelph, Ontario, Canada, pp. 69–79. IUCN Publications New Series, Supplementary Paper 39, Gland, Switzerland.
- McAllister, M. K., and Ianelli, J. N. 1997. Bayesian stock assessment using catch-age data and sampling-importance Resampling algorithm. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 284–300.
- McAllister, M. K., and Kirkwood, G. P. 1998. Bayesian stock assessment: a review and example application using the logistic model. *ICES Journal of Marine Science*, 55: 1031–1060.
- McAllister, M. K., Pikitch, E. K., and Babcock, E. A. 2001. Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 1871–1890.
- McAllister, M. K., Pikitch, E. K., Punt, A. E., and Hilborn, R. 1994. A Bayesian approach to stock assessment and harvest decisions using the sampling/importance resampling algorithm. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 2673–2687.
- NAMMCO North Atlantic Marine Mammal Commission 1995. Report of the Scientific Committee *ad hoc* Working Group on Atlantic Walrus, Copenhagen, 31 Jan–3 Feb 1995, Annex 2 of Report of the Third Meeting of the NAMMCO Scientific Committee. In NAMMCO Annual Report 1995, pp. 89–99. NAMMCO, Tromsø.
- NAMMCO North Atlantic Marine Mammal Commission 2002. Joint meeting of the Scientific Committee Working Group on the Population Status of Narwhal and Beluga in the North Atlantic and the Scientific Working Group of the Joint Commission on the Conservation and Management of Narwhal and Beluga, Annex 2, Report of the Ninth Meeting of the NAMMCO Scientific Committee. In NAMMCO Annual Report 2001, pp. 213–248. NAMMCO, Tromsø.
- Oh, M. S., and Berger, J. O. 1992. Adaptive importance sampling in Monte Carlo integration. *Journal of Statistics and Computer Simulation*, 41: 143–168.
- Outridge, P., Davis, W., Stewart, R., and Born, E. W. 2003. Investigation of the stock structure of Atlantic walrus (*Odobenus rosmarus rosmarus*) in Canada and Greenland using dental Pb isotope signatures derived from local geochemical environments. *Arctic*, 56: 82–90.
- Press, S. J. 1989. *Bayesian statistics: principles, models, and applications*. John Wiley, New York.
- Punt, A. E., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Review in *Fish Biology and Fisheries*, 7: 35–63.
- Raftery, A. E., Givens, G. H., and Zeh, J. E. 1995. Inference from a deterministic population dynamic model for bowhead whales. *Journal of the American Statistical Association*, 90: 402–430.
- Richard, P., and Campbell, R. 1988. Status of the Atlantic walrus, *Odobenus rosmarus rosmarus* in Canada. *Canadian Field-Naturalist*, 102: 337–350.
- Ross, W., and MacIver, A. 1982. Distribution of the kills of Bowhead whales and other sea mammals by Davis Strait whalers, 1829–1910. Unpublished Report for Arctic Pilot Project, January 1982, Available at Greenland Institute of Natural Resources, P.O. Box 570, DK-Nuuk, Greenland.

- Rubin, D. B. 1988. Using the SIR algorithm to simulate posterior distributions. *In* Bayesian Statistics 3, pp. 395–402. Ed. by J. M. Bernardo, M. H. DeGroot, D. V. Lindley, and A. M. Smith. Proceedings of the Third Valencia International Meeting, 1–5 June 1987. Clarendon Press, Oxford.
- Sease, J., and Chapman, D. 1988. Pacific walrus *Odobenus rosmarus divergens*. *In* Selected Marine Mammals of Alaska. Species Account with Research and Management Recommendations, pp. 17–38. Ed. by J. W. Lentfer Marine Mammal Commission, Washington, DC, USA.
- Tavrovski, V. 1971. Pinnipedia — Lastonogie. *In* Mammals of Yakutia, pp. 509–516. Ed. by V. A. Tavrovski. Nauka, Moscow, Russia. Translated from Russian by B. A. Fay and the late F. H. Fay, University of Fairbanks, Alaska.
- Teilmann, J., and Kapel, F. 1998. Exploitation of ringed seals (*Phoca hispida*) in Greenland. *In* Ringed Seals in the North Atlantic, pp. 130–151. Ed. by M. P. Heide-Jørgensen, and C. Lydersen. The North Atlantic Marine Mammal Commission, Tromsø, Norway.
- Udevitz, M. S., Gilbert, J., and Fedoseev, G. 2001. Comparison of methods used to estimate numbers of walruses on sea ice. *Marine Mammal Science*, 17: 601–616.
- 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. 1967. Arctic animals in relation to climatic fluctuations. *Meddelelser om Grønland*, 170: 1–227.
- Wade, P. R. 2002. A Bayesian stock assessment of the Eastern Pacific gray whale using abundance and harvest data from 1967–1996. *The Journal of Cetacean Research and Management*, 4: 85–98.
- Wiig, Ø., Gjertz, I., Griffiths, D., and Lydersen, C. 1993. Diving patterns of an Atlantic walrus (*Odobenus rosmarus rosmarus*) near Svalbard. *Polar Biology*, 13: 71–72.
- Witting, L. 1997. A General Theory of Evolution. By Means of Selection by Density Dependent Competitive Interactions. Peregrine Publisher, Århus, 330 pp.
- Witting, L. 2000. Population cycles caused by selection by density dependent competitive interactions. *Bulletin of Mathematical Biology*, 62: 1109–1136.
- Witting, L. 2003. Reconstructing the population dynamics of eastern Pacific gray whales over the past 150 to 400 years. *The Journal of Cetacean Research and Management*, 5: 45–54.