Polar Biol (2007) 31:69–75
DOI 10.1007/s00300-007-0334-7

ORIGINAL PAPER

Historical sex-specific distribution of Atlantic walrus (*Odobenus rosmarus rosmarus*) in Svalbard assessed by mandible measurements

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Received: 15 December 2006 / Revised: 29 June 2007 / Accepted: 29 June 2007 / Published online: 18 July 2007

Abstract We developed a discriminant function based on measurements of known-sex mandibles of walrus from the Canadian Arctic collected between 1983 and 1998 and used it to explore the sex ratio in the catches of walrus in Tusenøyane, south-eastern Svalbard, during the nineteenth century. Canadian mandibles older than 5 years of age of known sex were classified into correct sex with 100% accuracy by using two measurements. Applying the same discriminant function to 80 mandibles from Svalbard older than 5 years of age classified 48 (60%) as males and 32 (40%) as females. It also classified 584 aged and un-aged mandibles from Svalbard 67% (390) as males and 33% (194) as females. Eight of the aged jaws (10%) and 41 (7%) of the un-aged jaws had probabilities of classification into sex <80%. We stress the importance of being cautious in applying a discriminant function developed from Canadian mandibles to classify the sex of old weathered mandibles from Svalbard. However, we believe our results indicate that female walrus were once more common in south-eastern Svalbard than they are now.

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Keywords Atlantic walrus · *Odobenus rosmarus rosmarus* · Svalbard · Historical distribution · Morphometrics · Discriminant analysis · Sexual dimorphism · Mandible

Introduction

In 1604 the first hunt of Atlantic walrus (*Odobenus rosmarus rosmarus*) occurred in Svalbard (Poole 1604–1609), marking the beginning of the onslaught on the walrus population in this Arctic archipelago. By the middle of the nineteenth century the stock showed clear signs of decrease (Lamont 1861). The centuries of walrus hunting brought the reportedly large herds to the verge of extinction in Svalbard (Norderhaug 1969), until they finally were given total protection in 1952 (Anonymous 1952). It is difficult to assess the size of the original populations prior to hunting, but the Svalbard population must have been very large (Reeves 1978). Today the walruses at Svalbard and at Franz Josef Land in the western Russian Arctic are thought to comprise one common population (Gjertz and Wiig 1994; Wiig et al. 1996; Born et al. 2001).

Sexual segregation for part of the year is common in walruses (Fay 1985). However, in several areas in the Atlantic, male, females and young use the same terrestrial haul-outs in summer (e.g. Salter 1979; Miller 1982; Born et al. 1995). Most of the historic reports of walruses from Svalbard fail to mention the sex of the animals, and the information on distribution of females and calves in former days is accordingly scant (Gjertz and Wiig 1994). Chydenius (1865) wrote that walrus cows and calves at Svalbard were found in other areas than the bulls, and that walrus hunters thought the males travelled in big herds out to shallow water far from land, while the females with calves habitually stayed close to land and visited the fjords. Collett (1911–1912) also noted that walruses at Svalbard segregated into male and female herds. Today, however, most walruses observed at Svalbard are males (Born 1984; Gjertz and Wiig 1994). Summer and autumn observations after 1982 revealed females and calves in significant numbers only at the extreme north-eastern part of Svalbard. Walruses observed in other areas in summer were almost exclusively males, both adults and immature (Gjertz and Wiig 1994).

It might be that the distribution of sexes before the near extinction of the population at Svalbard was different than seen today. We address this question by investigating the sex of the remains of hunted walruses found in the south-eastern parts of Svalbard. Walruses have a high degree of sexual size dimorphism which is also clearly expressed in skull dimensions (Ognev 1935; Mohr 1942). Hence, sexual dimorphism in size is reflected in mandible size and form (Mohr 1942). Walruses at Svalbard are protected and present day material does not exist to quantify the dimorphism. We therefore developed a discriminant function (e.g. Wiig 1989; Hair et al. 1998) based on measurements of aged and sexed mandibles collected from the hunt in the Canadian Arctic and then used that function to explore the possible sex distribution in the remains left from the walrus catches in the Tusenøyane archipelago, south-eastern Svalbard, during the nineteenth century (Fig. 1).

Materials and methods

Eighty mandibles (33 females and 47 males) were collected between 1983 and 1998 in connection with monitoring of

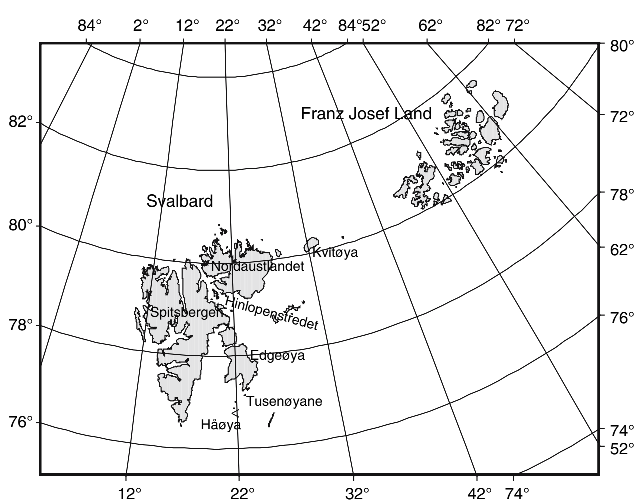

Fig. 1 Map of the Svalbard and Franz Josef Land archipelagos showing place names mentioned in the text

subsistence hunting activity in Hall Beach and Igloolik, on Foxe Basin, NT, Canada. These animals were aged by counting annual incremental layers in a lower canine tooth (Garlich-Miller et al. 1993). These mandibles were selected from a larger sample to represent an age range from 0 to 25–30 years in both sexes. Four measurements were taken of each mandible with a digital calliper and recorded to the nearest 0.1 mm (Fig. 2):

1. Mandible length (ML), distance between most anterior point on mandible and midpoint on posterior surface of articular condyle.
2. Mandible height (MH), distance between most dorsal point on coronoid process and most ventral point on angular process.
3. Least mandible depth (MD), minimal distance between dorsal and ventral mandibular surfaces, posterior to the last post-canine.
4. Least mandible thickness (MT), minimal lateral distance between medial and lateral mandibular surfaces, posterior to the last post-canine

The first three measurements are standard mandible measurements for walrus (F.H. Fay in lit. 1991) while the fourth was selected to express robustness of the mandible together with measurement 3.

In 1991 and 1992 we took the same four measurements with a manual calliper (recorded to the nearest 0.1 mm) on 591 mandibles found on terrestrial haul-outs on different islands in the Tusenøyane area of south-eastern Svalbard (about 77°N, 22°E). The mandibles derive from the catches that were made in this area mainly during the nineteenth century. These mandibles represented all samples found except those mandibles that were too degraded to be measured as decided subjectively in the field. Several of the measured mandibles were broken and did not provide all four measurements. Post-canine teeth were present in 83 mandibles and were collected for age determination (Stewart and Stewart 2005) using incremental layers in the cementum of the teeth (Garlich-Miller et al. 1993).

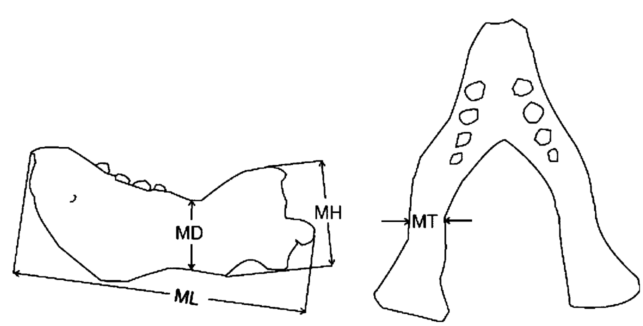

Fig. 2 Variable measured on mandibles of Atlantic walruses (*Odobenus rosmarus rosmarus*): *ML* mandible length, *MH* mandible height, *MD* least mandible depth, *MT* least mandible thickness

To restrict the analyses to animals in which most of the growth had ceased we explored the growth pattern in the four variables against age in bivariate plots based on the Canadian sample (not shown). From these plots it was clear that most of the mandibular growth of females had ceased in animals older than 5 years, while males continued to grow for several more years. Petersen and Born (1982) showed that male mandibles grow to the age of about 10 years. Female Atlantic walrus becomes sexually mature about 5 years (Born 2001) whereas males mature some years later (Born 2003). However, by age 5 years there was no overlap between males and females in the variable used and we restricted the analyses of the Canadian sample to individuals older than 5 years, which were 43 males and 29 females.

First we developed a discriminant function (Wiig 1989) using the Canadian material. The analysis considered differences in means, variances, and covariances of variables among groups. We selected variables in a stepwise manner, taking first the variable which made the largest contribution to the separation between the sexes according to the Mahalanobis distance. At each step, the variable that maximized the distance between the sexes was entered. Based on the variables entered the program calculated a classification matrix which indicated the power of the discriminant function. We also used the cross-validation method in which each case in the analysis was classified by the functions derived from all cases other than that particular case. We further used the Mahalanobis distance to calculate the probability that each case belonged to the predicted sex (see Hair et al. 1998; and http://www.statsoft.com/textbook/stathome.html.)

Discriminant analyses require variables that have a multivariate normal distribution and within-group variance-covariance matrices should be equal across groups (Hair et al. 1998). The variables were log transformed to secure normality and equality of variance-covariance matrices was tested by Box's M statistics. All analyses were conducted in SPSS for Windows (version 14.0).

Results

Mandibles of Canadian male walruses over 5 years old were significantly larger than females in all four measurements (untransformed) (Table 1; ML: $F_{1,69} = 174.0$, $P < 0.001$; MH: $F_{1,70} = 128.9$, $P < 0.001$; MD: $F_{1,70} = 220.1$, $P < 0.001$; MT: $F_{1,70} = 233.6$, $P < 0.001$). The stepwise discriminant analysis that included all four variables showed that the covariance matrices of the log-transformed data of the two sexes were not different (Box's $M = 0.601$, $df = 3$ and 158,041, $P = 0.90$). Of the four variables, MD and MT were selected because ML and MH did not contribute any additional discriminant power. The differences between the sexes in discriminate space was highly significant (Wilks' $\lambda = 0.162$, $X_2^2 = 125.4$, $P < 0.001$). The model accounted for 84% of the variation between sexes ($R = 0.92$). Based on MD and MT, none of the 72 Canadian mandibles was incorrectly sexed. The same result was achieved by cross-validation. The probability of classification to sex based on Mahalanobis distance was accordingly high for all individuals (Fig. 3).

The age of the Svalbard mandibles were between 5 and 30 years. Before we applied the discriminant function derived from the Canadian sample to the Svalbard material, we compared the relationship between the two variables in mandibles older than 5 years of age from Canada ($n = 72$) and Svalbard ($n = 80$) by linear regression of the log-transformed data (Fig. 4). There was a complete overlap of the data from the two areas and the regression coefficients were not significantly different ($F = 2.244$, df: 1, 148, $P > 0.05$).

Table 1 Descriptive statistics for four variables measured on mandibles of Atlantic walruses (*Odobenus rosmarus rosmarus*) older than 5 years from the Canadian Arctic

Variable (mm)	*n*	Males		*n*	Females	
		Mean	SD		Mean	SD
Mandible length	43	262.64	12.82	28	225.74	9.14
Mandible height	43	88.61	5.21	29	75.27	4.37
Least mandible depth	43	59.20	3.52	29	47.36	3.0
Least mandible thickness	43	25.24	3.0	29	15.31	2.17

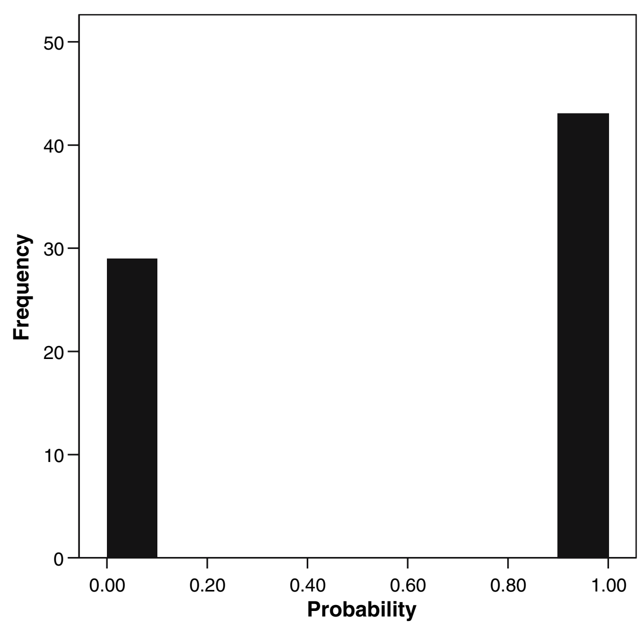

Fig. 3 Probability distribution of classifying 72 mandibles of Atlantic walrus (*O. rosmarus rosmarus*) from Canada as males based on a discriminant analyses and Mahalanobis distance from group centroid. Mandibles with probability < 0.50 are classified as females

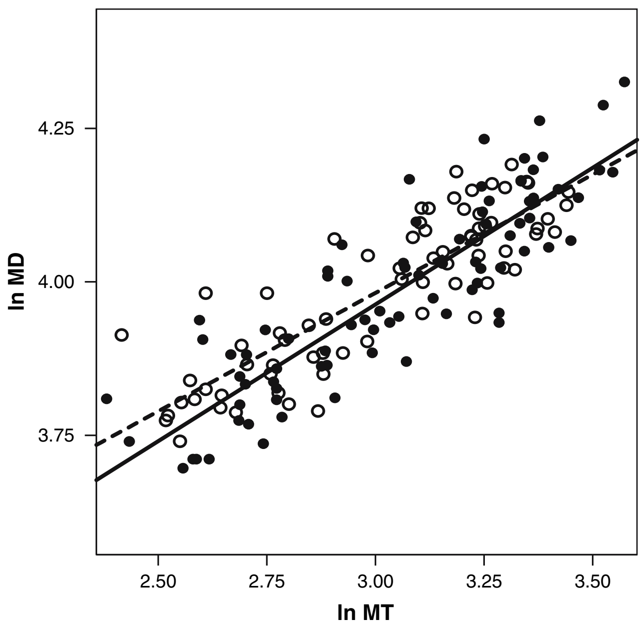

Fig. 4 Relationship between least mandible thickness (*MT*, mm) and least mandible depth (*MD*, mm) of Atlantic walrus (*O. rosmarus rosmarus*) older than 5 years of age from Canada (*open circles*) and south-eastern Svalbard (*filled circles*). *Dashed line* is the linear regression of Canadian data (ln MD = 0.386 ln MT + 2.825, $R^2 = 0.74$); *solid line* is the linear regression of Svalbard data (ln MD = 0.446 ln MT + 2.626, $R^2 = 0.76$)

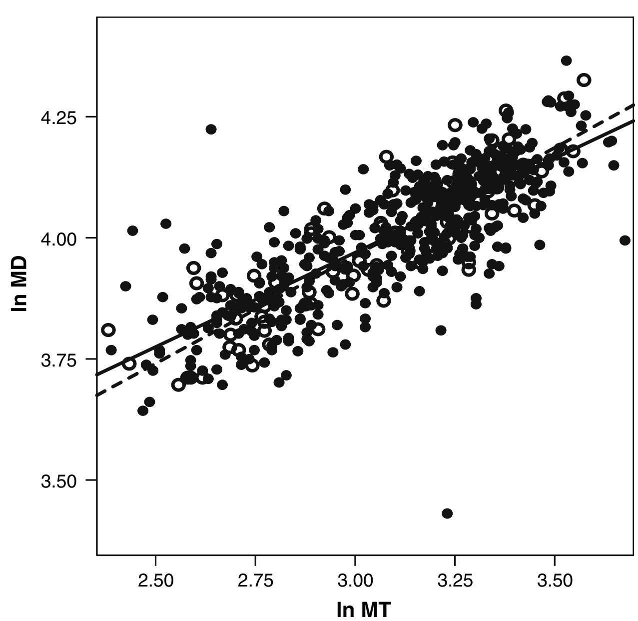

Fig. 5 Relationship between least mandible thickness (*MT*, mm) and least mandible depth (*MD*, mm) of Atlantic walrus (*O. rosmarus rosmarus*) from south-eastern Svalbard older than 4 years of age (*open circles*) and un-aged material (*filled circles*). *Dashed line* is linear regression of aged data (ln MD = 0.438 ln MT + 2.652, $R^2 = 0.76$); *solid line* is linear regression of un-aged data (ln MD = 0.391 ln MT + 2.798, $R^2 = 0.62$)

We also compared the relationship between the two variables in the aged (>4 years) ($n = 83$) and the un-aged ($n = 501$) Svalbard mandibles (Fig. 5). There was a complete overlap in distribution in the two samples and the regression coefficients were not different ($F = 2.090$, *df*: 1, 580, $P > 0.05$).

The discriminant function classified 48 (60%) of the 80 adult mandibles from Svalbard as males and 32 (40%) as females. Probability for sex classification was low (<80%) for eight (10%) mandibles (Fig. 6). We then classified all mandibles from Svalbard. Of the 584 mandibles on which the two measurements were taken, 390 (67%) were classified as males and 194 mandibles (33%) were classified as females. Also for these mandibles the probability of correct classification into sex was close to 0.50 for several mandibles (Fig. 7). Forty-one of them (7%) had probabilities <80%. The difference between sex distributions of the aged mandibles and all mandibles from Svalbard was not significant ($X_1^2 = 0.0093$, $P = 0.92$). Hence, the analyses indicate that female walrus were more common in south-eastern Svalbard in former days than today when very few adult females are observed in the same areas.

Discussion

Discriminant analysis is useful for building a predictive model of group membership based on observed characteristics of each case. The procedure generates a discriminant

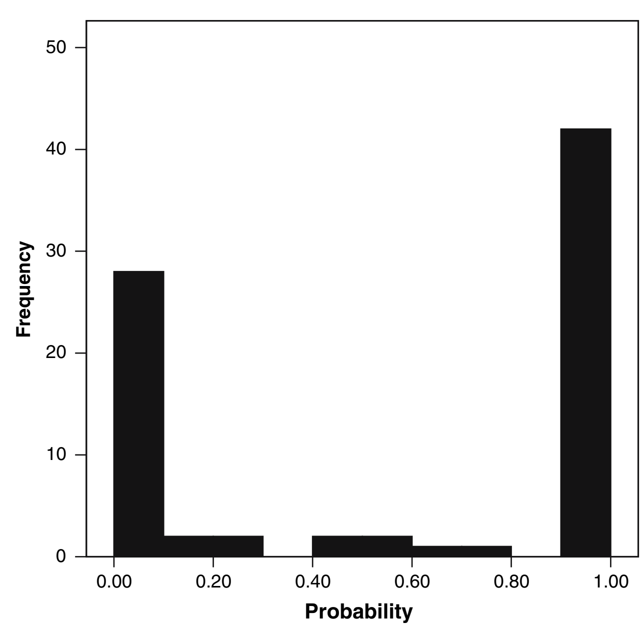

Fig. 6 Probability distribution of classifying 80 mandibles of Atlantic walrus (*O. rosmarus rosmarus*) older than 5 years from the Tusenøyane area, south-eastern Svalbard, as males based on a discriminant analyses and Mahalanobis distance from group centroid. Mandibles with probability < 0.50 are classified as females

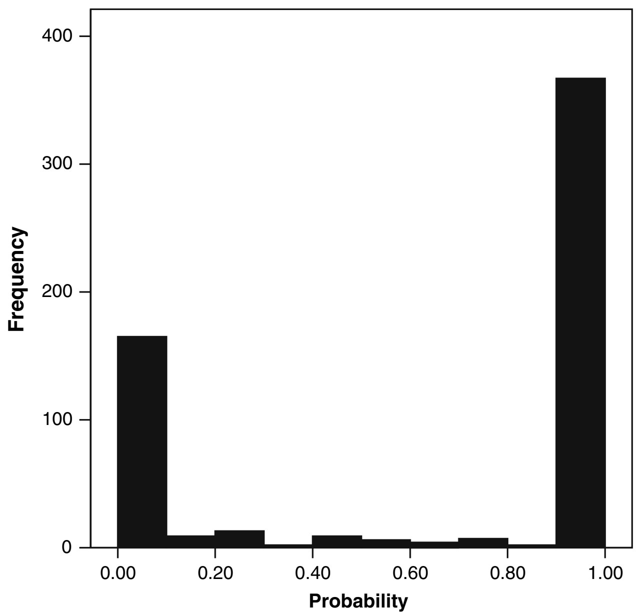

Fig. 7 Probability distribution of classifying 584 mandibles of Atlantic walrus (*O. rosmarus rosmarus*) from the Tusenøyane area, south-eastern Svalbard, as males based on a discriminant analyses and Mahalanobis distance from group centroid. Mandibles with probability < 0.50 are classified as females

function based on linear combinations of the predictor variables that provide the best discrimination between the groups. The functions are generated from a sample of cases for which group membership is known; the functions can then be applied to new cases that have measurements for the predictor variables but have unknown group membership (Hair et al. 1998, http://www.statsoft.com/textbook/stathome.html

The analysis discriminated the sexes of the Canadian mandibles with 100% accuracy. The same high frequency was achieved using the cross validation technique in which each case is classified by the functions derived from all cases other than that particular case. This agreement of independent techniques is a measure of the reliability of the function. Early in the process of exploring the data we even detected an individual for which the wrong sex was recorded in the original material. The correct sex was later confirmed by molecular techniques (methods not reported here).

Garlich-Miller and Stewart (1998) investigated body growth in walruses from Foxe Basin collected in the 1980s–1990s and found them to be larger than walruses collected from Hudson Bay in the 1950s. The body length had a similar growth pattern to walruses collected in north-western Greenland (taken from Knutsen and Born 1994), and was within one SE for the asymptote of males selected for large size in Svalbard (Wiig and Gjertz 1996). This indicates that there might be differences in allometric growth among areas so that a sex identification tool developed on one set of data must be used with caution on a set of data from other times and areas. However, there were no allometric difference between samples from Canada and Svalbard supporting the application of the discriminant function developed on Canadian material to the material from Svalbard. The larger spread in probability distributions (Figs. 6, 7) might partly reflect the uncertainty of applying the Canadian discriminant function to the Svalbard material. Most of the material is, however, classified to sex with a high probability.

After more than 100 years on the ground the Svalbard mandibles were weathered to some degree. The bone structure of the walrus mandible is very dense, the periosteal zone in particular, due to the age-related accumulation of layering in this zone (Petersen and Born 1982). We therefore assume that the two measurements used for sexing (MD and MT) were not influenced by weathering to any great extent. If there were a bias, it would make the mandibles smaller than they had been in the living animals, thereby increasing the probability of wrongly classifying males as females. However, ML and MH were more worn by weathering and the use of them for sexing would have been more uncertain. Application of the discriminant function on un-aged mandibles might, also, lead to young males (<5 years old) being classified as females. However, the age distribution of the aged material (>4 years) and the overlap in size distribution of the aged and the un-aged material (Fig. 5) indicate that there are few very young individuals in the material. Misclassification of young males as females is not believed to be a significant concern in the analysis. We therefore believe that the results reflect that there actually were many females in the catches (ca. 33%).

All the mandibles from Svalbard were collected in the Tusenøyane archipelago. Most of the hunting here probably took place in the period 1800–1899 (Gjertz and Wiig 1994; Lønø 1972). It is difficult to determine the hunting period in which our material originated exactly. However, 502 out of 591 mandibles were from one island, Håøya, the scene of one of the most famous slaughters of walruses in Svalbard. It occurred in 1852 and is well documented. The exact number of walruses present on the island at that time is not known for certain, but is believed to have counted several thousand, many hundreds of which were killed in 1 day (Guernsey 1861). After this time the island was used rarely by walruses (Guernsey 1861; Lamont 1861) even into the twentieth century (Gjertz and Wiig 1994). It is therefore likely that the mandibles measured at Håøya predominantly are remains of the 1852 slaughter. This also means that females and males were found on the same haul-out. This situation is not uncommon for Atlantic walrus (Salter 1979; Miller 1982; Born et al. 1995) and is also known for the Pacific walrus (*O. r. divergens*) at Wrangel Island (e.g. Ovsyanikov et al. 1994) but contrasts with Chydenius (1865) and Collett (1911–1912) who noted that walruses at Svalbard segregated into male and female herds in summer.

We cannot be certain that the sex proportion in these land catches reflect the sex proportion of the walruses in the area. Lamont (1861) described that hunters often caught females with young at ice floes in the Tusenøyane area. These were butchered at the floes and would not turn up in our samples. Such a bias would mean that the proportion of females in the area was higher than the ~33% we detected. Similarly, present day catches in western Greenland and Foxe Basin are about 33–40% females (Orr et al. 1986; Born et al. 1995) and if present, such a bias in the 1800s would result in an underestimate of the proportion of females present in Svalbard, increasing the difference with current population structure.

The limited information on the historical distribution of females with calves in Svalbard indicates mother-calf pairs centred on four main areas: north-western Spitsbergen, Hinlopenstretet, north-eastern Nordaustlandet-Kvitøya, and southern Edgeøya-Tusenøyane (Gjertz and Wiig 1994). In the recent past, after 1982, the only area where females with young have been observed in significant numbers is the extreme north-eastern part of Svalbard. The herds of walruses observed in other areas in summer are almost exclusively juveniles and adult males (Born 1984; Gjertz and Wiig 1995).

The walruses in the Svalbard-Franz Josef Land area today belong to a recovering population (Gjertz and Wiig 1994, 1995). Sealers caught large numbers of walruses in Franz Josef Land in the late nineteenth century. In 1897, almost all those caught were females with young, with a few young bulls (Southwell 1898). From about 1,900 sealing vessels caught large numbers of walruses in Franz Josef Land (See Gjertz et al. 1992 for a review), predominantly females and calves. Bruce and Clarke (1898) similarly found few males in Franz Josef Land in summer. In recent years, while limited at Svalbard, large herds of females with calves have been documented at Franz Josef Land (Born et al. 1995).

Our results indicate that mature female walrus were once more common in south-eastern Svalbard than they are at present. It appears that Franz-Josef Land served as a refuge for females during the years of extreme exploitation at Svalbard but that females have not re-established themselves on Svalbard as successfully as have males. This might be expected based on the tendency for males to roam more widely than females (Andersen and Born 2000; Stewart et al. 2003). The catches we have analysed were taken during the so-called "Little Ice Age", which were the coldest period during the whole Holocene (ACIA 2005). The ice conditions were severe and much different from today. The effect the changed ice conditions might have on the distribution of sexes and on the recovery of walrus populations in the Svalbard-Franz Josef Land area remains unclear.

Acknowledgments We thank Kathy Fisher, Joel Garlich-Miller and the walrus hunters of Igloolik and Hall beach for collecting walrus jaws in Canada. Ages of Canadian material was done by Barb Stewart. Svalbard material was aged by Bjørn Bergfødt and Kjell A. Fagerheim. Ryan Stewart assisted with the Canadian measurements and drawing (Fig. 2). We are thankful to all. Funding in Canada was provided by the Department of Fisheries and Oceans. Funding in Norway was provided by the Research Council of Norway (grant no.: I 735.004), the Norwegian Polar Institute, and the Natural History Museum, University of Oslo.

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