Life history and ecology of harbour porpoises (*Phocoena phocoena*) from West Greenland

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ABSTRACT

During 1988, 1989 and 1995, 187 harbour porpoises (*Phocoena phocoena*) were sampled from the catches off West Greenland. The samples were taken in 3 areas between 62° N and 70° N: northerly (*n*=134, Maniitsoq and locations Kangaamiut, Qeqertarsuaq and Qasigiannguit further north), southerly (*n*=30, Nuuk) and southernmost (*n*=23, Paamiut). A suite of biological measurements and data were collected from these samples. Comparison of age and length distributions between years and areas indicated that while there were no statistical differences between the Maniitsoq and northerly samples in different years, the southerly Nuuk and Paamiut samples were biased to younger age classes. Application of the Gompertz growth model to length and weight at age data indicated an asymptotic length of 154 cm in females and 143 cm in males with weights of 64 kg and 52 kg respectively. A number of correlations were observed between length, mid-girth (G_3), body and blubber weights and blubber thickness. Indicators of body condition showed that overall pregnant females were fattest but that blubber thickness was greatest in juveniles. The blubber lipid content was generally 92-95% wet weight of tissue. Stomach content analysis for 92 animals indicated regional differences, although capelin (*Mallotus villosus*) was predominant in all samples. The presence of fish, squid and crustaceans indicated opportunistic feeding. Females ovulated from age 3-4 years at a length of about 140 cm; combined testis weights >200 g indicated maturation in males from age 2 years upwards at a length >125 cm. Several small embryos were found, consistent with a mating season in late summer. Testis hypertrophy in August also supported a late summer breeding. Analysis of ovarian *corpora* indicated annual ovulation. Certain biological parameters, including body condition indicators, indicate differences between West Greenland and eastern North Atlantic populations that agree with published genetic findings.

Lockyer, C., Heide-Jørgensen, M.P., Jensen, J. and Walton, M.J. 2003. Life history and ecology of harbour porpoises (*Phocoena phocoena*) from West Greenland. *NAMMCO Sci. Publ.* 5:177-194.

INTRODUCTION

The harbour porpoise, *Phocoena phocoena*, is among the most abundant and widespread of the North Atlantic cetaceans. In West Greenland the species is found from the southern tip to the northernmost inhabited areas in Avanersuaq, with a main distribution between 62° N and 66° N

(Teilmann and Dietz 1998). Porpoises have been taken as bycatch, as elsewhere throughout the coastal areas bordering the North Atlantic (IWC 1996), and in West Greenland they were occasionally taken in drift netting operations for salmon. Christensen and Lear (1977) estimated that 1,400 harbour porpoises were caught in the non-Greenlandic driftnet fishery for salmon in 1972. This fishery ceased during the 1970s and today harbour porpoises are primarily taken by Inuit hunters and fishermen from West Greenland settlements for food (Fig.1). There are very few catches off the east coast, the majority occurring off southern and central western Greenland. The reported catches up to the early 1990's peaked at about 1,500 animals for the whole of Greenland, but have generally remained between 500-1,000 animals per year, with an increasing trend during the 20th century (Teilman and Dietz 1998). The reported catches between 1993 and 1997 inclusive (Piniarneq 1999, 2000) totalled 8,286 with a range of 1,418 to 1,824 per year.

The life history and ecology of this species is not well known off West Greenland, despite several studies in other geographical regions in the North Atlantic. This study describes current life history and basic features of the biology of harbour porpoises from West Greenland, and makes comparisons with populations from adjacent areas. It is hoped that the information will provide a baseline for future monitoring in West Greenland.

MATERIALS AND METHODS

During July through September in 1988 and 1989, and again in August and September 1995, animals were sampled from 3 locations between 62° N and 69° 30´ N: the northerly location Maniitsoq (129) including Kangaamiut, Qeqertarsuaq and Qasigiannguit (5), and 2 southerly locations, Paamiut (23) and Nuuk (30) in southwestern Greenland (Fig. 2). The animals were shot at sea, and, in 1988 and 1989, were mainly bought at the local game market in Maniitsoq. Intact carcasses were rare so that often only jaws and teeth were available. In 1995, animals were purchased from hunters and

Fig. 1. *Harbour porpoise meat, skin and heads are sold for food at a Greenlandic marketplace. (Photo: Lars Witting)*

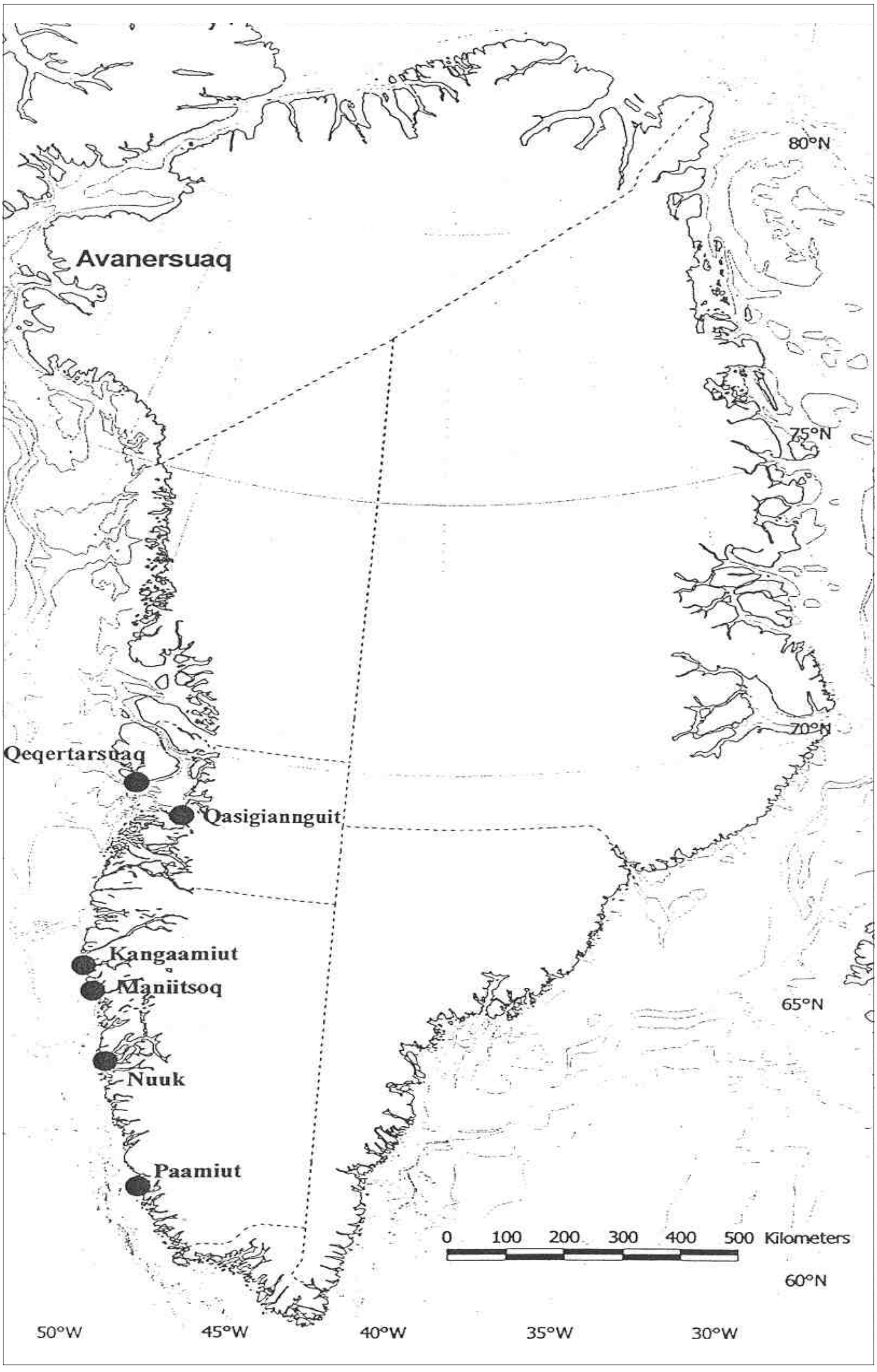


Fig. 2. *Map of Greenland showing sites mentioned in the text.*

frozen whole at the harbours for later examination. The muktuk (blubber and trimmed underlying 1 cm blubber only) which is highly prized as food, was removed from these latter animals and weighed for calculating the commercial value of the carcass. All data relating to whole body and organ weights, body fat condition and stomach content originate from 1995.

Age determination

Teeth (usually about 5) were collected from lower jaws in 1995 (sample size of 103 individuals). Two from each individual were decalcified in *RDO* (a proprietary decalcifying agent), sectioned on a freezing microtome at 25 micron thickness through crown and central pulp cavity (1 rotated 90° relative to the other) and stained with Erhlich's acid haematoxylin (Lockyer 1995a). Similar methods (Kremer 1987) were used on the earlier teeth samples (81 individuals). Growth layer groups (GLGs) were counted in both dentine and cementum under low power magnification with transmitted light. GLGs were taken as representing years (Bjørge *et al.* 1995; Lockyer 1995a, b). Age used in the analyses was equivalent to the number of complete GLGs counted, so that most animals were older than this age by perhaps about 3 months if, as elsewhere in the North Atlantic, peak births occur in June (Lockyer 2003). All tooth sections were read by 2 readers, independent of biological information about the specimen. Agreement was reached on all age determinations, the tooth GLGs being exceptionally clear and unambiguous in West Greenland porpoises (mostly Type 1 - Lockyer 1999). Age distributions by sex and area were compared.

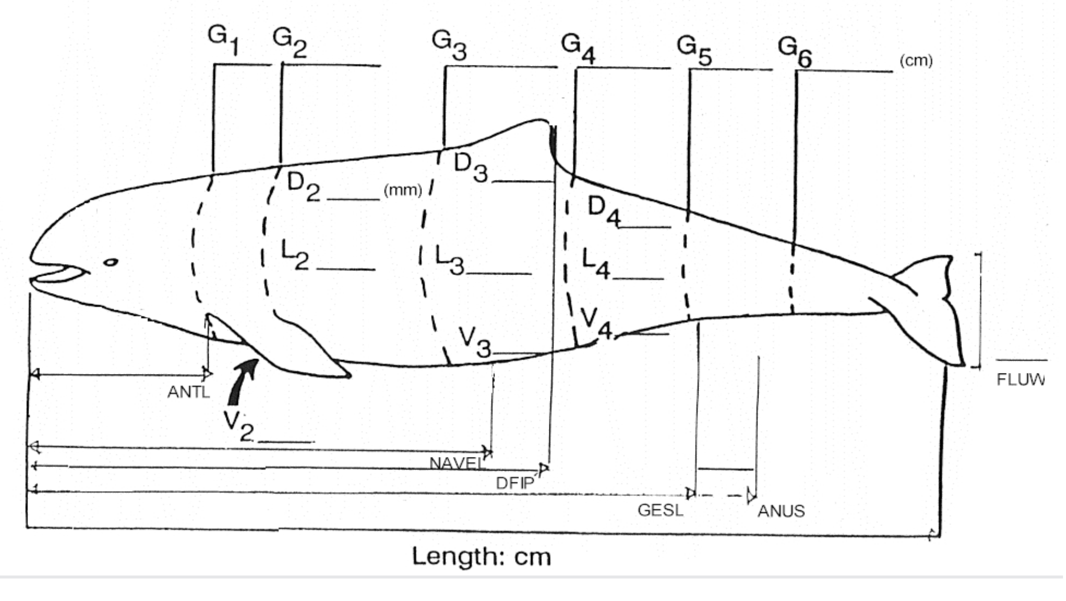
Growth in length and weight

Body length was measured in the standard way in a straight line parallel to the carcass from tip of the lower jaw to the notch in the tail flukes (Fig. 3). Body size at age by sex was investigated, and growth curves (Kaufmann 1981) were fitted to the data using the Gompertz model, where least square estimation of the parameters was made with Gauss-Newton minimisation in the nonlinear least-squares algorithm of S-Plus (Math Soft Inc.).

Reproduction

Gonads were collected from all porpoises in 1995 and from a few in earlier years. The testes (for 55 individuals) were weighed and measured for volume, and the ovaries (for 56 indi-

Fig. 3. *Diagram of the standard measurements and sampling sites on harbour porpoise.* G_1-G_6 *are girths,* D_2-D_4 *are dorsal,* L_2-L_4 *are lateral and* V_2-V_4 *are ventral blubber thicknesses. Other length measurements indicated are taken in a direct straight line and not along the body curve.*



viduals) weighed and examined for the presence of *corpora lutea* and *c. albicantia* (Perrin *et al.* 1984) as indicators of sexual maturity and reproductive status (Read and Hohn 1995). Ovarian *corpora*, detected from the surface scar on the ovaries, were cut open, measured for diameter and classified according to type by examination under a binocular microscope. All ovaries were fixed in 10% neutral buffered formalin, and sliced in 1 mm thick sections.

The epididymides in males were checked for the presence of sperm. Some testis samples (1 cm slices) collected and fixed in 10% neutral buffered formalin during 1988 and 1989, were also examined histologically. In females, the uterine horns were opened and the presence of an embryo was noted, and the mammary glands were checked for expression of milk. Estimates of mean age and length at sexual maturation were obtained.

Body fat condition

Measurements were collected according to a scheme (Fig. 3). Body girths and blubber thicknesses (measured vertically excluding skin and any leaf fat underlying the blubber) were measured in addition to length. Body weight, blubber, muscle, skeletal and organ weights were taken. Samples of blubber, from skin through to underlying muscle, were also taken and analysed for lipid content as percentage of wet weight. The lipid was extracted using chloroform/methanol (Folch *et al.* 1957).

Diet

Stomachs were weighed full and empty to establish food intake, and the contents washed out and sorted in large Petri dishes. Food items were identified to species by otolith, eye lens, skeletal remains, squid beaks and identifiable soft parts, using reference material both at the Greenland Institute of Natural Resources and the Zoological Museum in Copenhagen.

RESULTS AND DISCUSSION

Age determination

The age data from the 2 time periods 1988-9 and 1995 were provided by different readers, but nevertheless were found to be comparable after all earlier tooth specimens were reread by Lockyer. Therefore, all age data from Maniitsoq and the northerly areas in 1988-9 were combined with the 1995 Maniitsoq age data (Lockyer *et al.* 2001). The number of age samples from Paamiut and Nuuk in 1995 was small. Since these 2 areas are more southerly, the samples were combined, and included 2 animals from 1988-9.

The age frequency distribution for Maniitsoq and the northerly areas by sex, indicated a modal age class of 1-2 years in females and 2-3 years in males with a maximum age of 14 in females and 17 in males (Lockyer *et al.* 2001). The combined Paamiut and Nuuk age samples, however, showed a modal age of 0 years in both sexes, with a longevity of 12-13 years in females and 9-10 years in males (Lockyer *et al.* 2001). For females the mean age (± S.E.) was 3.37 ± 3.04 in Maniitsoq and 3.03 ± 3.21 in Nuuk and Paamiut combined. For males, the mean age was 4.90 ± 3.90 in Maniitsoq and 2.43 ± 2.55 in Nuuk and Paamiut (Lockyer *et al.* 2001). These mean ages were compared using t-tests (Zar 1984). For females there was no significant difference between Maniitsoq and the 2 southerly regions, while there was a significant difference found for males between Maniitsoq and the other regions combined ($t = 3.469$, $P < .001$, $df = 58$).

In general, the data indicated that the age strucuture for females in the northerly and southerly samples were similar, but in males the southerly sample contained predominantly young animals, while the northerly sample comprised more older and mature animals. The reason for this may be due to age-, sex- or maturity-related segregation in the population. It has certainly been reported that distributional patterns of males may differ from that of females in the North Sea area (Walton 1997) based on mt DNA analyses, and seasonal variations in distribution and movements by sex have been reported in the Skagerrak area (Kinze 1985, 1990). However, one may also consider the effect of different hunting pressures in the 2 regions, or a potential seasonal effect on distributional segregation. The time of year when these samples were taken closely approximates the breeding season which might arguably be anticipated to

Table 1. Growth parameters (± S.E.) fitted to length (cm) at age (years) data in West Greenlandic harbour porpoises, using a modified (Lockyer *et al.* 2001) Gompertz model $[Lt = Lw \exp(- b \exp(- k t))]$. Sample sizes are 81 for males and 71 for females.

Parameter	Females	Males
Lw (asymptotic body length)	153.978 ± 2.615	141.547 ± 1.426
b (constant)	0.482 ± 0.024	0.389 ± 0.023
k (exp. coefficient)	0.563 ± 0.071	0.591 ± 0.067

have some effect. In harbour porpoises the usual breeding season is late summer (see reproductive results below, also Sørensen and Kinze 1994, Lockyer 1995b, c, Lockyer 2003, Lockyer and Kinze 2003).

The longevity of up to 17 years is similar to that seen in eastern Canada where there is a history of bycatches (Read and Hohn 1995). It is lower than the 24 years reported for the British Isles (Lockyer 1995b, c) where most animals sampled are strandings, and Denmark where ages >20 years have been recorded from both strandings and bycatches (Lockyer and Kinze 2003).

Growth in length and weight

Body length

Length frequency distributions for the northerly samples in both time periods were comparable, and therefore combined by sex (Lockyer *et al.* 2001). Mean lengths (± S.E.) and size ranges of females from Maniitsoq, and Nuuk and Paamiut are similar at 129 ± 3.5 cm (80-164 cm) and 129.3 ± 4.6 cm (70-169 cm) respectively. The equivalent northerly and southerly length frequency distributions and size ranges for males, showed that mean lengths are significantly different at 130.7 ± 2.1 cm (80-159 cm) for Maniitsoq and 122.8 ± 3.4 cm (90-144 cm) for the southerly regions (Lockyer *et al.* 2001). The length range in the 2 regions is broadly similar, although in females the minimum length is lower and the maximum length is higher in the south. In males the opposite occurs, with a lower minimum and higher maximum in the north, although samples are smaller in the south. Combined regions by sex are shown in Fig. 4 (after Lockyer *et al.* 2001). The largest and smallest females are 166 cm and 74 cm respectively with a mean of 129.1 ± 2.8 cm; and in males largest and smallest are 158 cm and 84 cm respectively with a mean of 128.2 ± 1.8 cm.

When length at age is plotted in the 2 regions by sex, there is no apparent difference, and therefore the length at age data have been combined for both time periods and all areas by sex separately (Fig. 5, after Lockyer *et al.* 2001). We have fitted length at age growth curves to these data,

Table 2. Comparison of age- and size-related biological parameters in different populations of harbour porpoises, modified after Lockyer *et al.* (2001).

Region and period of sampling	Mean age at sexual maturity, in yr		Mean length at sexual maturity, in cm		Mean adult length, (Lw), in cm		Reference
	Male	Female	Male	Female	Male	Female	
West Greenland							
1988-1995	2 - 2.45	2.95 - 3.6	127	138-142	141.5	154	this study
Eastern Canada							Read and Gaskin (1990)
1969-73	>3	3.97	134	147	146	163	Read (1990a)
1985-88	?	3.44		143	144	155	Gaskin *et al.* (1984)
British Isles	3	3 - 4	130-135	140-145	145	160	Lockyer (1995b, c)
1985-1994							
Denmark	3 - 4	3.3	135	143	145	160	Lockyer and Kinze (2003)
mainly 1980-1998							Sørensen and Kinze (1994)

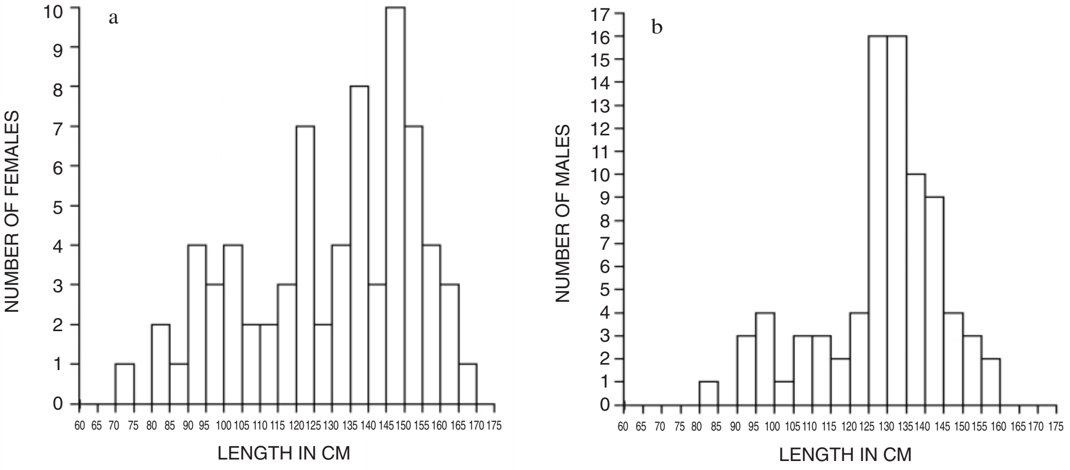


Fig. 4. *Length frequency distributions for a) female porpoises, and b) male porpoises, from 3 regions of West Greenland (1988, 1989 and 1995) .*

and the growth parameters are presented in Table 1. The Gompertz growth model indicates an asymptotic length of about 154 cm in females and 141.5 cm in males. These lengths are smaller than those reported for harbour porpoises off the British Isles (mainly North Sea) and eastern Canada (Table 2). It is difficult to compare the results directly because asymptotic length has been determined in different ways in each region. However, a reanalysis using only lengths of animals 8 years and older from West Greenland, the British Isles and Denmark shows no significant differences when 95% confidence intervals are calculated: females: West Greenland – sample too small; British Isles: 150.78 – 168.13 cm (*n*=11); Denmark: 156.22 – 161.587 cm (*n*=31); males: West Greenland: 138.78 – 147.54 cm (*n*=9); British Isles: 141.62 – 150.54 cm (*n*=13); Denmark: 139.49 – 144.73 cm (*n*=52). Lengths calculated in this way are not necessarily representative of predicted asymptotic lengths as calculated by Bertalanffy or Gompertz methods.

Body weight

Body weight was plotted against age for both sexes combined. The asymptotic body weights,

Fig. 5. *Length at age curve for female porpoises (n=85) (a), and male porpoises (n=91) (b), from 3 regions of West Greenland (1988, 1989 and 1995) with fitted Gompertz growth curves.*

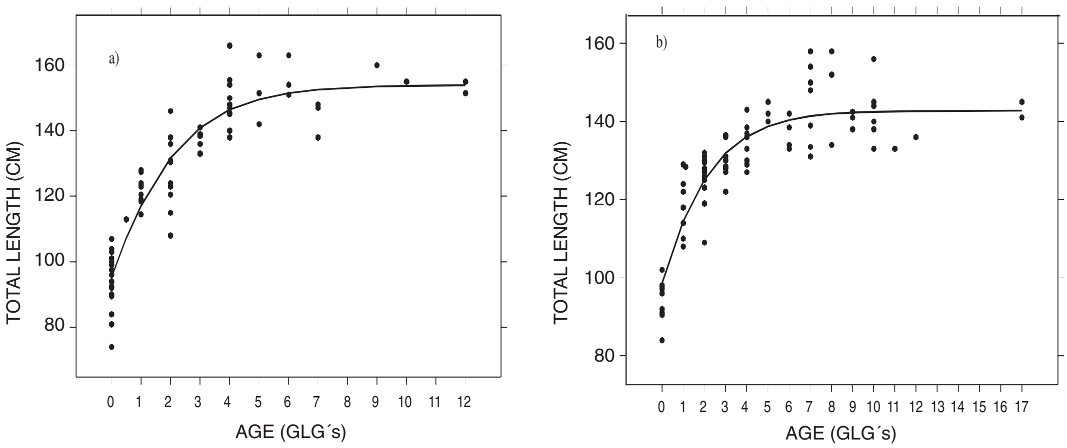


Table 3. Growth parameters (± S.E.) fitted to weight (kg) at age (years) data in West Greenlandic harbour porpoises, using the Gompertz model [Wt = Ww exp(- b exp(- k t))].

Parameter	Females	Males
Ww (asymptotic body weight)	64.391 ± 1.960	51.177 ± 1.824
b (constant)	0.401 ± 0.013	0.309 ± 0.024
k (exp. coefficient)	0.391 ± 0.030	0.460 ± 0.066

calculated using the Gompertz model (Table 3), are 64 kg and 51 kg for females and males respectively (Figs. 6). Few reports of harbour porpoise record body weight. However, in a comparison of asymptotic weights with animals from British waters (Lockyer 1995b), where females and males were 55 kg and 50 kg respectively, West Greenlandic harbour porpoises appear heavier. Recent data for Danish porpoises (Lockyer and Kinze 2003) show higher adult body weights than British ones (65 kg in females and 50 kg in males), and are more similar to Greenlandic porpoises. The British data were obtained from primarily stranded animals whereas Danish animals, of similar body length, were mainly known to be bycaught and were generally fatter than the British counterparts. Nevertheless the East Atlantic porpoises reach a larger adult body length so that weight might be expected to be larger than that for Greenland, thus suggesting that Greenlandic porpoises are relatively fat. Another factor that suggests that Greenlandic animals are fatter for length is that the sample comes only from a narrow time window in late summer, whereas other areas have been sampled year-round. Lockyer *et al.* (2000, 2003) report that there is a marked variation in body weight of Danish porpoises because of seasonal fat deposition with a peak in winter and low in summer. Thus it is possible that the Greenlandic porpoises may also have a seasonal cycle of weight variation in which case their body weight in late summer would not be maximal and might even be at a low and not reflect an even greater weight difference with porpoises from elsewhere. The relative fatness of the animals will be discussed further below.

Organ and tissue weights

Various organ and tissue weights are expressed as mean (± S.E.) together with the range and percentage body weight in Table 4. These include blubber, muscle, skeleton (including skull, pectoral flippers and tail flukes), lungs, liver, heart, kidneys, pancreas and spleen. The average proportions of blubber and muscle are

Fig. 6. *Weight at age curves for female (a) and male (b) porpoises from 3 regions of West Greenland (1995) with fitted Gompertz growth curves. Females: n=46,* $W = 0.00028\ L^{1.713}\ G_3^{0.782}$. *Males: n=55,* $W = 0.00008\ L^{1.570}\ G_3^{1.212}$.

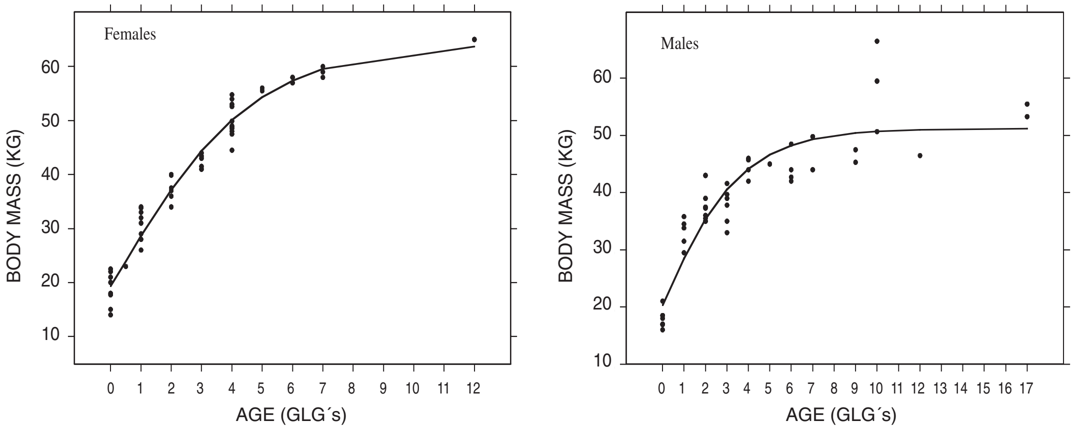


Table 4. Organ and tissue weights expressed as mean ± S.E., percentage of body weight and actual range.

Measurement / Tissue / Organ (measurement unit)	Sample Size (n)	Mean ± S.E.	% Mean body weight	Range Min	Max
Body length (cm)	102	128.9 ± 1.8		89.5	166.0
Body weight (kg)	100	38.5 ± 1.3	100.00	14.0	66.5
Skeleton incl. skull and flukes (kg)	101	6.4 ± 0.2	16.62	3.0	19.3
Blubber (kg)	101	12.8 ± 0.3	33.25	7.2	14.0
Muscle (kg)	100	11.4 ± 0.5	29.61	3.2	25.3
Lung – left (g)	98	426.2 ± 15.4	1.11	131.0	805.0
Lung –right (g)	97	461.5 ± 17.2	1.20	162.0	896.0
Liver (g)	96	1258.3 ± 50.2	3.27	213.0	2360.0
Heart (g)	97	309.1 ± 11.6	0.80	100.0	590.0
Kidney - left (g)	98	160.8 ± 6.1	0.42	55.0	348.0
Kidney – right (g)	96	160.4 ± 6.1	0.42	51.0	346.0
Pancreas (g)	94	102.9 ± 10.2	0.27	10.0	950.0
Spleen (g)	41	7.7 ± 0.7	0.02	1.0	23.0

33.3% and 29.6% respectively for average subadult size (Table 4) compared to 33.4% and 22.6% respectively for a smaller sample of adult Canadian Bay of Fundy porpoises (Yasui and Gaskin 1986), and 26-29% and 23-31% respectively for a similar sample size of adult British porpoises (Lockyer 1995d). By all accounts the British animals appear lean compared to the West Greenlandic and Canadian porpoises.

It is clear that muscle mass increases exponentially with growth of the animal, whereas blubber mass increase is less dramatic and the relationship with length is almost linear (Figs 7 and 8). In Table 5, the blubber and muscle weights have been expressed by sex and maturity, and by adulthood the proportions of the 2 tissues are approximately equal with perhaps slightly more muscle (30.4% blubber and 32.2% muscle in males and 31.1% blubber and 30.8% muscle in females), whereas the blubber is greater than muscle mass by up to almost 2 times in juveniles. This is similar to observations by Lockyer (1995d) for British porpoises. This fat provides a large energy reserve for the juvenile who may be less successful in foraging initially.

Regarding organ weights (Table 4), the right lung is consistently heavier than the left, while kidney size is similar on both sides. Referring to organ - body weight relationships for mammals (Brody 1968) the kidney and other organ

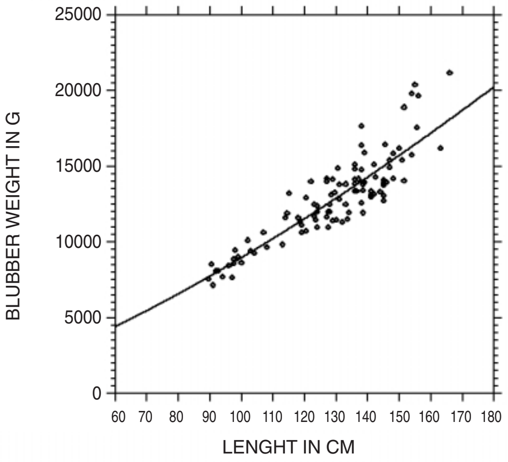


Fig. 7. Blubber weight at length in female and male harbour porpoises, from 3 regions of West Greenland (1995).

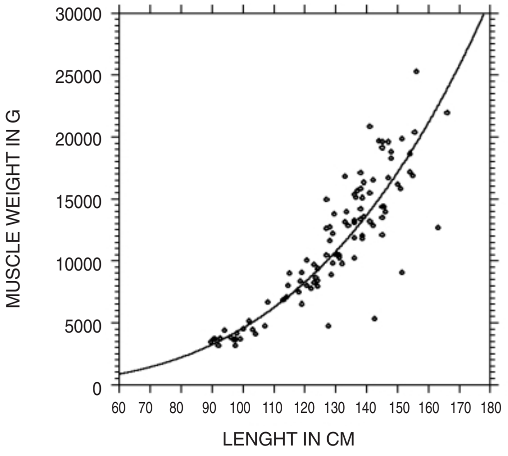


Fig. 8. Muscle weight at length in female and male harbour porpoises, from 3 regions of West Greenland (1995).

Table 5. Mean body size parameters ± S.E. and indicators of body fat condition for immature and mature female and male harbour porpoises from West Greenland.

Sex and Maturity Category	Length (cm)	Body weight (kg)	Blubber weight (kg)	Muscle weight (kg)	Mid-girth, G_3 (cm)	Mid-dorsal, blubber D_3, thickness (mm)	Mid-lateral blubber, L_3, thickness (mm)	Blubber lipid content % wet weight blubber
MALES								
Immature (*n*=14)	107.42 ± 3.75	24.55 ± 2.20	10.04 ± 0.51	5.52 ± 0.58	74.93 ± 2.04	29.62 ± 1.11	26.93 ± 0.84	92.64 ± 0.66
Mature (*n*=31)	135.45 ± 1.28	43.47 ± 1.31	13.21± 0.27	14.01 ± 0.71	90.95 ± 1.11	24.53 ± 0.65	22.37 ± 0.49	93.39 ± 0.35
FEMALES								
Immature (*n*=29)	117.03 ± 3.20	29.96 ± 1.89	11.35 ± 0.45	8.00 ± 0.67	80.50 ± 1.78	27.12 ± 0.70	25.79 ± 0.55	92.48 ± 0.79
Mature – pregnant (*n*=22)	148.91 ± 1.70	52.95 ± 1.30	16.45 ± 0.46	16.32 ± 0.68	95.52 ± 1.29	27.43 ± 0.67	23.86 ± 0.55	95.55 ± 0.43

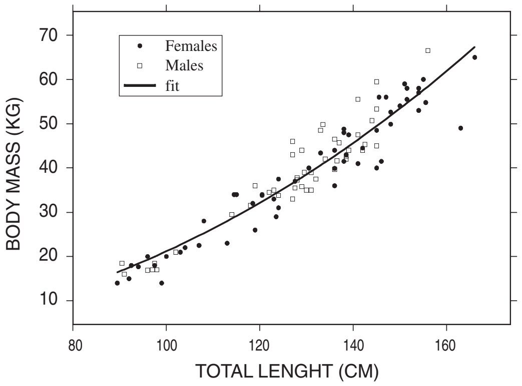


Fig. 9. *Body weight (W) at length (L) for females and males combined, all areas, where* $W = 0.00058\ L^{2.281}$. *Standard error for the exponent is ± 0.092, standard error of constant is ± 0.00026, n =103.*

weights appear to be close to those predicted for this size of mammal, including heart and lung weights, excepting the liver which appears heavier than predicted. Unfortunately we do not have estimates of blood weight which has generally been found to be greater in marine compared to terrestrial mammals (Elsner 1999) and is connected to the former's diving ability. It should also be noted that skeletal weight is biased by remnants of muscle, and therefore is heavier than actual.

Body fat condition

Body weight at length

Fig. 9 shows weight at length relationships for males and females. Comparison with similar weight at length relationships for other areas (Lockyer 1995c, d, Lockyer and Kinze 2003) indicates that while the British and Danish porpoises are similar, the West Greenlandic porpoises are consistently heavier for their length. By adulthood, differences are not apparent in healthy animals of similar size, with an adult of 150 cm weighing 53.1 kg off Denmark and 53.3 kg off West Greenland, but only 44.4 kg in stranded and probably old or sick animals off the British Isles.

Body weight at length and girth

Body weight and mid-girth (G_3) measurements were highly correlated (R^2 >0.96 in males, 0.88 in females). Further investigation found a better correlation between length, mid-girth and weight, than for weight and either length or girth alone. Weight can be predicted from length-girth and weight equations:

1) Males $W = 0.00008\ L^{1.570}\ G_3^{1.212}$

where W = body weight in kg, L = body length in cm, and G_3 is mid-girth in cm. Standard error for the exponent of L is ± 0.206, G_3 is ± 0.211, standard error for the constant is ± 0.00005, $n = 44$

2) Females $W = 0.00028\ L^{1.713}\ G_3^{0.782}$

Standard error for the exponent of L is ± 0.190, G_3 is ± 0.238, standard error for the constant is ± 0.00017, $n = 47$.

The weight estimation is improved by inclusion of the mid-girth factor, as it takes into account the body fat condition of the animal, especially since there is more girth variation in females.

Girth and blubber weight and thickness

There appears to be a positive linear relationship between mid-girth and body length (Fig. 10). However, a plot of mid-dorsal (D_3) blubber thickness (mm) on length (cm) – similar to mid-lateral (L_3) blubber thickness on length, has an inverse correlation with a negative exponent:

3) Males $D_3 = 1507\ L^{-0.843}$

Standard error for the exponent of L is ± 0.142; standard error for the constant is ± 1.991

4) Females $D_3 = 45.6\ L^{-0.108}$

Standard error for the exponent of L is ± 0.109; standard error for the constant is ± 1.702.

It appears that blubber thickness is greater in juveniles than adults, especially in males. This is reflected in the decreasing mass of blubber relative to body size (Fig. 6 and Table 5). Blubber weight can be predicted from length (L in cm) and blubber weight (B in kg) equations:

5) Males $B = 0.03597\ L^{1.202}$

Standard error for the exponent of L is ± 0.098; standard error for the constant is ± 0.00161.

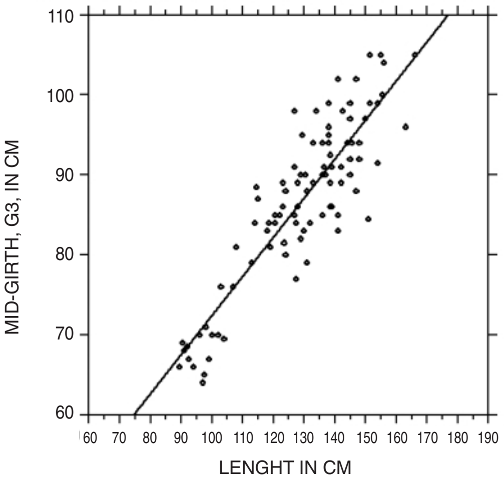


Fig. 10. *Mid-girth, G_3, at length for female and male porpoises, all areas.*

6) Females $B = 0.00995\ L^{1.477}$

Standard error for the exponent of L is ± 0.075; standard error for the constant is ± 0.00117.

Clearly blubber mass increases with body size, but is relatively less in larger and older animals. The excess blubber may be unnecessary for insulation and may be less important as energy reserves in adults.

Indicators of body condition such as girth (mid-girth, G_3) and blubber thickness (mid-dorsal, D_3), showed that the pregnant females were generally fattest (Table 5), as reported from eastern Canada (Read 1990b) and the British Isles (Lockyer 1995c, d). Animals were not only heavier but fatter for length than the British animals (Lockyer 1995c, d) and fatter than the Canadian animals (Read 1990b) as shown in Table 6. The fact that the porpoises in West Greenlandic waters are generally living in water close to freezing year-round, the fatness, especially noted in calves, may contribute to insulation and survival. However, we should point out that the sample was exclusively from the autumn, and we do not know what the fatness factor may be at other times of year. For this reason, observed differences may not necessarily be meaningful overall, even if significant differences can be demonstrated.

Blubber lipid content

The blubber lipid content for West Greenland

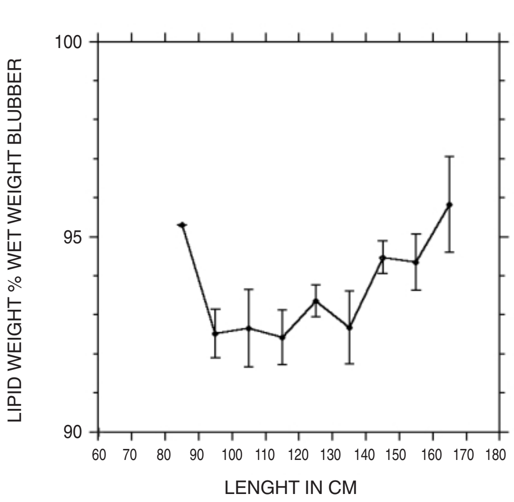


Fig. 11. *Mean ± S.E. percentage wet weight of blubber lipid in harbour porpoises.*

animals was generally 92-96% of wet weight of tissue (Table 5), a higher level than for British animals (83-87%) (Lockyer 1995c, d). However, as already noted, the latter sample comprised many strandings. There is a small yet significant increase in blubber lipid content with increase in body length (Fig. 11) when a regression is fitted, (ANOVA F ratio = 3.990, df = 97, P = .049), in part because of the transition from immature to mature (L>140 cm) and also because the highest lipid content is found in large mature females. The single high level in the 80-90 cm range may be an anomalous individual.

Diet

Stomach content analysis was performed on 92 animals, of which 78 had identifiable remains. The presence of fish, squid and crustaceans indicated opportunistic feeding (Table 7). The analysis indicated regional differences, although capelin (*Mallotus villosus*) was predominant in all samples, as reported off north Norway (Aarefjord *et al.* 1995) and Iceland (Víkingsson and Sigurjonsson MS 1996), in contrast to the predominantly demersal species consumed off Denmark and Sweden (Aarefjord *et al.* 1995, Lockyer and Kinze 2003). In the North Sea, a variety of fish are consumed comprising mainly gadoids and sandeel (*Ammodytes* sp.), but no capelin (Lockyer and Kinze 2003).

The number of prey items other than capelin was relatively low (Fig. 12). A recent study (Møller *et al.* in press) of fatty acid profiles in blubber of porpoises from West Greenlandic and Danish North Sea shows significant differences, reflecting the different diets in each region.

Reproduction

Male

Testis weights have been recorded, but no histological examination has consistently been made for the presence of sperm, spermatogonia or tubule diameter and character (open / closed), and could therefore not be used. Lockyer (1995b) however, used the criterion of combined testis weights >200 g as a guide to sexual maturation.

Table 6. Measurements (means) for adult porpoises. Females include pregnant but not lactating, and lactating and pregnant females.

Region	Mean length of sample, in cm		Blubber weight, in kg		Girth, mid-girth G_3, in cm		Blubber thickness,in mm		Reference
	Male	Female	Male	Female	Male	Female	Male	Female	
West Greenland	135.5	148.9	13.2	15.8	91.0	95.5	22.4 (L_3 position)	23.9	this study
							23.9 (V_2 position)	25.8	this study
Eastern Canada	141	146	13.5	16.2	91.8	95.4	17.5 (V_2 position)	19.6	Read (1990b)
British Isles	144.5	150.4	11.9	12.6	90.5	88.7	17.7 (L_3 position)	14.0	Lockyer (1995c, d)

Table 7. Food preferences of harbour porpoises in West Greenland. The percentage of stomachs with each prey item is given for the 3 districts (sample size in parentheses). The total number of stomachs with prey remains was 78.

Species	Maniitsoq (*n*=41) %	Nuuk (*n*=25) %	Paamiut (*n*=11) %
Mallotus villosus	93	100	91
Boreogadus saida	42	60	55
Sebastes sp.	24	20	9
Reinhardtius hippoglossoides	5	4	9
Ammodytes sp.	2	24	9
Liparis sp.	5	12	0
Lycodes sp.	0	0	9
Squid beaks or eyes	37	12	9
Pandalus sp.	2	0	0
Parathemisto libellula	10	8	36
Euphausiids	7	20	27

Testis weight and sexual maturity

Combined testis weights plotted against age and length (Lockyer *et al.* 2001), using the 200 g criterion, indicated the switch from immature to mature at 2 years and showed that all males are mature at 3 years. Maturation occurs from a length of 123 cm and all males are mature at a length of 130 cm (Lockyer *et al.* 2001). The average age at sexual maturation is 2.45 years as calculated using DeMaster (1978). These data are compared with data for harbour porpoises from elsewhere (Gaskin *et al.* 1984, Lockyer 1995b) and with estimates for Danish porpoises (Sørensen and Kinze MS 1990, 1994, Lockyer and Kinze 2003) in Table 2.

Female

Presence of *corpora* was used to determine ovu-

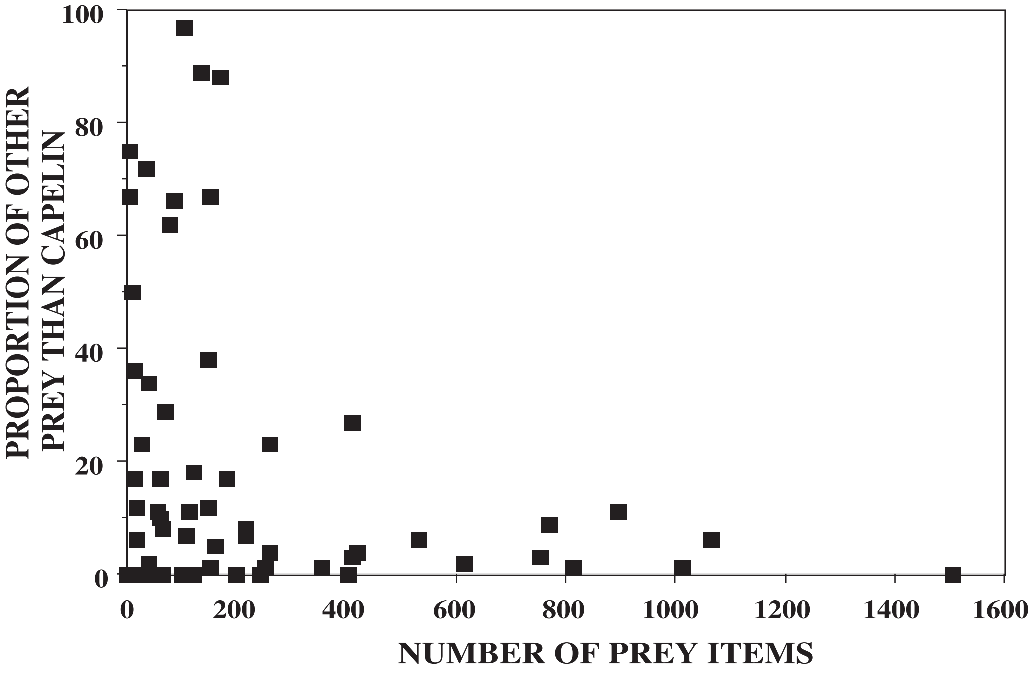


Fig. 12. *Frequency of prey items in the stomachs of harbour porpoises, all areas.*

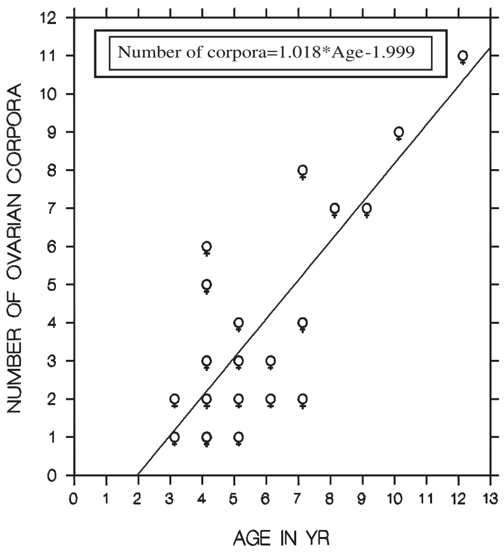


Fig.13. *Total corpora number at age for female porpoise, all areas.*

lation rate from a linear regression of corpora number at age, excluding all females with zero *corpora*. An estimation of mean age at sexual maturation was made using the method of DeMaster (1978).

Ovarian *corpora* and sexual maturity

The presence of at least 1 *corpus luteum / albicans* was used as a criterion for sexual maturity (Lockyer 1995b, c). Other criteria used for assessing maturity were evidence of pregnancy and/or lactation. The youngest animal with a *corpus* in this sample of 31 was 3 years old, and the oldest recorded was 12 with 11 *corpora.* A regression analysis of ovarian *corpora* number against age was performed for 30 animals (Fig. 13, and Lockyer *et al.* 2001) excluding an obvious outlier of age 12 with only 2 *corpora*. Only females with at least 1 *corpus* indicating at least 1 ovulation / pregnancy were included in this calculation regardless of whether or not it was a *corpus luteum* or *albicans*. Accordingly, at first ovulation, the line cuts the age axis at 2.95 years:

7) Number of corpora = 1.018• Age - 1.999

Standard error of the coefficient is ± 0.142; standard error for the constant is ± 0.838.

The implied ovulation interval is thus about 1 year. The data indicate a strong seasonality of reproduction (see below), thus females probably ovulate each year about the same month. The coefficient above has a S.E. of ± 0.142, so that the ovulation interval could fall in the 95% confidence interval range of 0.76 to 1.38 years. The mean estimate falls in the same range as that observed for Danish (Lockyer and Kinze 2003) and Canadian Bay of Fundy (Read 1990a) porpoises, but indicates more strongly annual reproduction if the outlying female individual is excluded.

An estimation of mean age at sexual maturation (first ovulation) was made using the method of DeMaster (1978), and was found to be 3.6 years. This is higher than the intercept of the *corpora* at age regression, but fits better with the observation in this data set that no female has a *corpus* before age 3.

Reproductive parameters appear to be consistently lower than those reported for porpoises from British and Danish waters (mainly North Sea) and eastern Canada (Table 2). In males, length and age at maturation are less than those reported (130-135 cm and 3 years or more) in the North Sea area (Lockyer 1995b, Lockyer and Kinze 2003) and off eastern Canada (Gaskin *et al.* 1984). In females, the age at maturation is similar to porpoises elsewhere in the North Atlantic (Gaskin *et al.* 1984, Read 1990a, Read and Gaskin 1990, Read and Hohn 1995), but size is smaller than the 140-147 cm reported elsewhere (Gaskin *et al.* 1984, Read and Gaskin 1990, Lockyer 1995b, Lockyer and Kinze 2003).

Breeding season

Despite the narrow sampling season (July to September), testis weights were found to increase significantly during August (Lockyer *et al.* 2001). This is consistent with findings from other areas of the North-East Atlantic where a similar hypertrophy has been reported in August (Sørensen and Kinze 1994, Lockyer 1995b, c, Lockyer and Kinze 2003), and suggests that mating, and probably conception, may be especially likely at this time. Sperm were found in all males >129 cm and in one 128 cm length in a sample of 15 males collected during August 1989 and early September. However, the inferred breeding and calving periods differ from the Canadian Bay of Fundy harbour porpoise where testicular activity peaks in late

June and the main calving season is May (Read 1989).

Foetuses
Several small embryos (sample of 10) of a size consistent with approximately 6-8 weeks developmental age were found in 1995, mainly in September, consistent with a mating season in late summer.

DISCUSSION

Biological parameters and longevity are generally close to or within the ranges of those reported for populations in other geographical areas. However, there is some indication that sexual maturation may occur at a slightly younger age and smaller size than elsewhere.

The data on body size for harbour porpoises from West Greenland indicate that these animals are generally smaller in length than porpoises in the eastern North Atlantic but also off the Canadian Atlantic coast, while body weight is relatively heavier. In addition, body fat condition measured by blubber mass, relative girth and blubber thickness as well as lipid content of blubber suggests that the Greenlandic porpoises are fatter than their counterparts elsewhere. It is not yet clear whether or not this phenomenon may in part be attributable to a seasonal effect because the Greenlandic sample is from a short summer period. We would argue however, that this explanation is unlikely if comparisons are made with live porpoises monitored in Danish waters. Over more than 2 years of observation, pronounced seasonal increases in body fat were found in the winter with decreases in spring and lows in summer (Lockyer *et al.* 2000, 2003). If a similar seasonal pattern held for West Greenlandic porpoises their winter body weight would be even greater.

Differences between West Greenland and eastern North Atlantic populations are supported by the genetic findings from allozyme and DNA-micro-satellite analyses that, in a comparison of West Greenland with inner Danish waters and the North Sea, indicated probable sub-populations (Andersen 1993, Andersen *et al.* 1995, 1997, 2002). Differences between West Greenland and eastern Canadian porpoises may also indicate population separation (Rosel *et al.* 1999), although Gulf of St Lawrence porpoises do not differ genetically from West Greenland (Tolley *et al.* 2001). Additional new information on harbour porpoise tooth ultrastructure in different regions of the North Atlantic, indicates clear differences between West Greenland and the Canadian Bay of Fundy, and also with eastern North Atlantic populations (Lockyer 1999). Furthermore, Lockyer (1999) reported differences in tooth structure between Maniitsoq and more southerly areas (Nuuk and Paamiut), which could not be explained by arguments for sex or age segregation. Møller (unpublished) has recently shown further differences between porpoises from Maniitsoq, and Nuuk and Paamiut, based on fatty acid signatures in the blubber of the same animals from 1995 examined in this paper. While these differences may be argued as transient and a reflection of local feeding ecology, the teeth nevertheless demonstrate a permanent record.

There is evidence therefore, from a variety of sources, that suggests that the West Greenland population may be distinct from populations in other geographical areas. Internal inconsistencies in age distribution also suggest a possible seasonal sex and age segregation.

ACKNOWLEDGEMENTS

The authors particularly wish to thank Jeppe Møhl, of the Zoological Museum, Copenhagen, for help in the dissections; and numerous other colleagues in Greenland, Denmark and other countries who have contributed to the sampling and data gathering at different times.

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