Growth, reproduction, age structure and feeding habits of white whales (*Delphinapterus leucas*) in West Greenland waters

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Reproductive organs, mandibular teeth, stomach contents and body measurements including total mass from white whales (*Delphinapterus leucas*) taken by Inuit hunters in West Greenland during 1985–1992 were analysed. Both sexes of white whales from West Greenland attain a greater length at physical maturity than do white whales from Alaska, Hudson Bay, northern Québec, the White Sea and the Kara Sea. Male white whales attain sexual maturity at 6–7 years. Size of testes and presence of spermatozoa suggest that mating takes place in May or perhaps later. Female white whales apparently become sexually mature at 4 to 7 years of age, but the negative bias of age estimates from whales whose teeth lack the neonatal line confounded our effort to estimate the age at sexual maturity. Gestation lasts at least 330 days, with implantation in May–June, and calves are likely to be born in April–May. The oldest white whales were taken in spring in Disko Bugt, whereas the herds taken in the Upernavik area in autumn usually consisted of immature whales and females with calves. The white whales taken in the current fishery in West Greenland are significantly smaller than those taken in the drive fishery in South Greenland in the 1910s and 1920s. The most likely explanations include changes in age distribution caused by the harvesting regime and changes in prey availability on the wintering grounds. Present diet of white whales in West Greenland includes polar cod (*Boreogadus saida*), arctic cod (*Arctogadus glacialis*), squids (Cephalopoda), and lanternfishes (Myctophidae) in the Upernavik area in the autumn and redfish (*Sebastes* sp.) and squids in Disko Bugt in the spring.

Key words:
White whale, beluga, *Delphinapterus leucas*, Greenland, growth, reproduction, age structure, feeding habits.

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Introduction

The white whale or beluga (*Delphinapterus leucas*) has been an important game animal in the Inuit hunting societies that have inhabited the west coast of Greenland for more than 2000 years. Nowadays it is among the most important of the marine mammals exploited in Greenland, and the annual catch of 500–1000 white whales often exceeds the combined catch of all other whale species in Greenland (Heide-Jørgensen 1990).

White whales arrive in the municipality of Upernavik (Fig. 1) in October during their southward autumn migration, and they are killed there in large numbers in a drive fishery (Heide-Jørgensen 1994). The present-day center

of winter distribution of white whales off West Greenland is along the coast between 67°N and 69°N; white whales are rarely observed more than 70 km offshore (Heide-Jørgensen *et al.* 1993). The return spring migration northward begins in April when white whales are caught along the ice edge or in the loose pack ice of Disko Bugt (Kapel 1977). In May-June they are taken in open water in the Vaigat, northern Disko Bugt. The small catches during spring along the ice edge in Uummannaq, Upernavik and Avanersuaq municipalities suggest that the white whales cross Baffin Bay somewhere between Disko and the municipality of Avanersuaq on their migration to the eastern Canadian High Arctic.

Despite its historic and current importance in the Greenlandic subsistence economy, the life history and
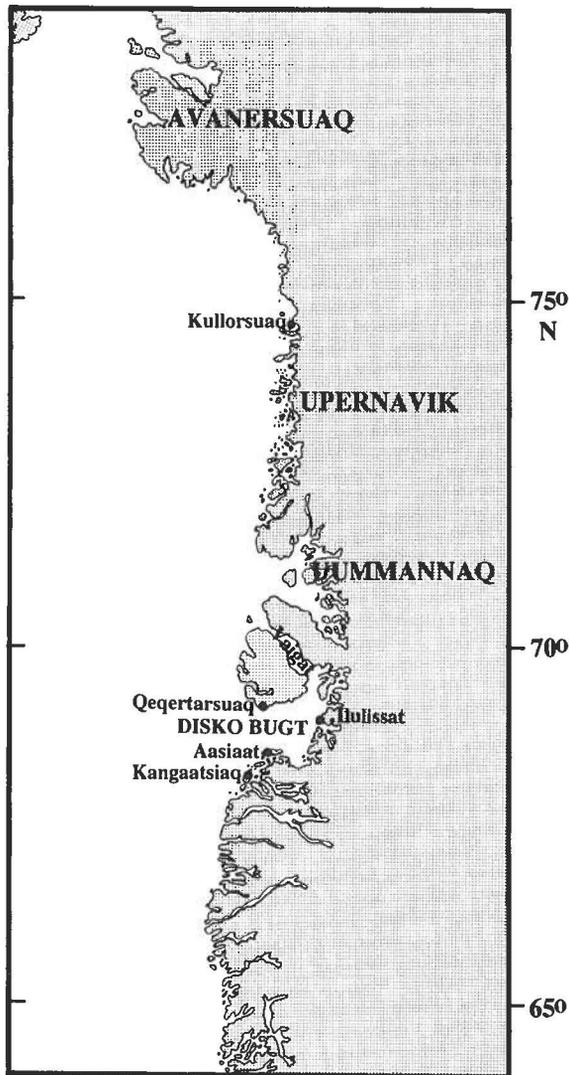
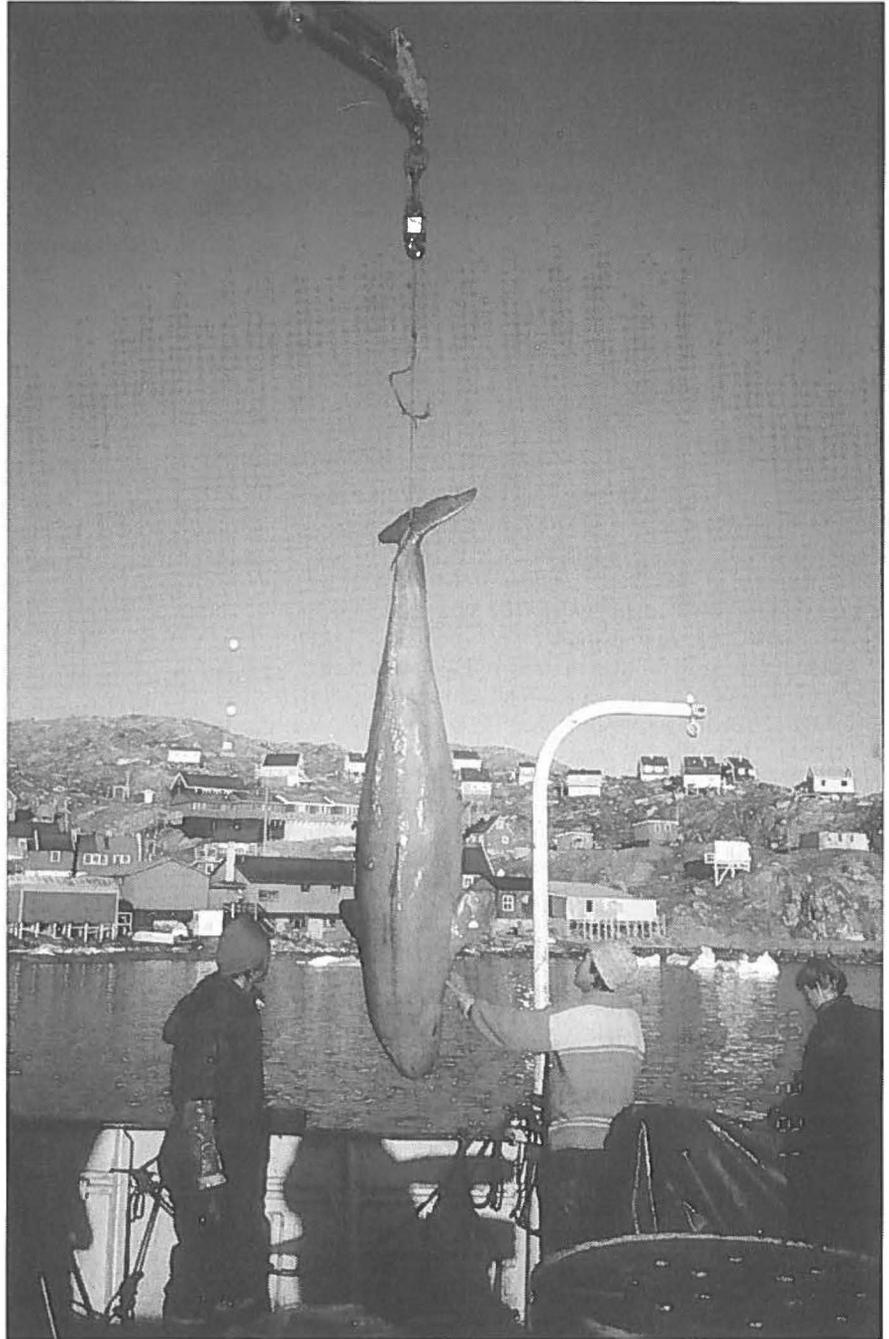Fig. 1. Map of municipalities, settlements and sites mentioned in the text.

population structure of this white whale population is poorly documented. Degerbøl & Nielsen (1930) studied body growth and exploitation of white whales caught in a drive-net fishery in southwestern Greenland (south of 66°N), an area where these whales were formerly abundant (Heide-Jørgensen 1994). The history of white whale exploitation in Greenland has been described by Kapel (1975, 1977, in Reeves & Mitchell 1987) and Heide-Jørgensen (1994). Aerial surveys conducted in 1981, 1982, 1990 and 1991 documented the occurrence and population decline of white whales wintering off West Greenland (McLaren & Davis 1983, Heide-Jørgensen et al. 1993).

The present study was initiated to provide basic biological information on growth, maturation, reproduction, diet and age structure of white whales off West Greenland. Some of these features are compared with the results from similar studies in Alaska (Burns & Seaman 1986), Hudson Bay (Sergeant 1973, Doidge 1990a), northern Québec (Doidge 1990a) and the Sea of Okhotsk (Kleinenberg et al. 1969), and to results of similar but unpublished studies in the White and Kara seas (G.N. Ognetov, SEVPinro, Arkhangelsk, unpubl. data). Growth parameters are also compared with data for white whales taken in southwestern Greenland in the 1910s and 1920s (Degerbøl & Nielsen 1930).

Materials and methods

Samples from 381 white whales were collected from the Inuit catch in West Greenland during 1985–1992 (Table 1). The samples were collected by biologists who were present during flensing of the animals or by hunters trained to collect the samples.

Table 1. Samples collected from white whales in West Greenland, 1985-1992. Sex was not determined for all specimens. "Drive fishery" indicates whales were driven into shallow bays. "Ice entrapment" indicates whales were caught when trapped in the ice. "Ice edge" indicates whales were caught in spring primarily along the diffuse ice edge in Disko Bay and in the loose pack ice during breakup of fast ice.

Year	Month	Municipality	No. males	No. females	Total	Catch method
1985	October-November	Upernavik	13	20	35	Drive fishery
1986	March	Kangaatsiaq	7	0	7	Ice edge
1989	April	Qeqertarsuaq	6	0	6	Ice edge
1989	October	Upernavik	30	22	54	Drive fishery
1990	February	Ilulissat	7	6	13	Ice entrapment
1990	March-April	Aasiaat	3	7	10	Ice edge
1990	May	Ilulissat	5	0	5	Ice edge
1990	October	Upernavik	43	86	132	Drive fishery
1991	October-November	Upernavik	38	57	95	Drive fishery
1992	April-May	Qeqertarsuaq	15	7	24	Ice edge
TOTAL			167	205	381	

Fig. 2. Weighing of white whale onboard the research vessel *Adolf Jensen* in Kullorsuaq.

External examination and body measurements

Standard body length (SL) was measured to the nearest cm in a straight line along the side of the whale from the anterior tip of the lower jaw to the notch of the tail flukes. Dorsal curvilinear length was measured on a subsample of whales for comparison with SL. While being mea-

sured, the carcasses were lying on their sides on the beach. Fluke width (FW) was measured from tip to tip of the flukes in a straight line, also to the nearest cm. For some whales SL could not be obtained, but was calculated from the regression of FW on SL (see Fig. 8, later). Length of nipples and presence of exudates were noted, and mammary glands were examined for milk.

Between 30 September and 4 October 1991 measurements of total body mass were made of 97 white whales

killed at Kullorsuaq in the municipality of Upernavik (Fig. 1). The entire, unopened whales were lifted aboard r/v *Adolf Jensen* using a crane (Fig. 2). They were then weighed to the nearest kilogram with a Salter DC-2 digital scale and length was measured when the whales were lying on the deck. Body mass and length were measured in the same way for three male and one female white whales killed at Qeqertarsuaq (Godhavn) between 9 and 14 May 1992.

Sex was determined by chromosomal analysis (Palsbøll *et al.* 1992) for 32 whales for which no reproductive organs were collected.

Age estimation

Teeth were extracted from lower jaws and stored frozen. Longitudinal sections of 150–200 µm were cut with a diamond wafering blade mounted on a Buehler Isomet lowspeed saw. If necessary, sections were polished by hand using wet 600 grit silicon carbide paper disks (3M) before microscopic examination.

Counting of growth layer groups (GLGs) was facilitated by the use of a transmitted light microscope (Carl Zeiss Jenaval) with polarization (see Heide-Jørgensen *et al.* 1994). Two trained readers examined all teeth independently. The mean of their combined counts of GLGs was used to estimate age. The term "complete age" is used for tooth sections in which all GLGs, including the neonatal line, could be counted. "Minimum age" refers to those teeth which did not contain a neonatal line because the apex of the tooth was worn. Two GLGs were assumed to be accumulated during one year (Heide-Jørgensen *et al.* 1994).

Growth of white whales from the Kara and White seas

For comparison with growth in white whales from West Greenland, data on growth of white whales from the Kara and White seas from G.N. Ognetov (SEVPinro, Arkhangelsk) were analysed. Length and age were estimated in similar ways as for the Greenland samples for 164 males and 40 females from the White Sea and 148 males and 218 females from the Kara Sea. A preliminary presentation of a subset of these data was given by Ognetov (1981).

Statistical analysis of growth data

Foetal length at age was described by a second-order polynomial. Length and body mass at age of *post-partum* whales was fitted to the following growth models:

von Bertalanffy:
$$SL = L_\infty * (1 - b * exp(-k * x))$$
Gompertz
$$SL = L_\infty * (exp(-b * exp(-k * x)))$$
General Growth Equation:
$$W = W_\infty * (exp(-b * exp(-k * x)))^M$$

where SL is the standard length, W total body mass, L_∞ asymptotic standard length, W_∞ asymptotic body mass, and x age in years prorated for months, and where b, k and M are constants to be derived. The geometric relationship between standard length and body mass can be described as:

$$body\ mass = a * SL^b$$

where a and b are constants to be fitted.

Least-square estimation of parameters was carried out using the Quasi-Newton minimization in the Nonlin procedure of Systat (Wilkinson *et al.* 1992).

Male and female reproductive organs

Length, width, thickness and mass of testes and epididymides were measured. Right and left testes and epididymides were not distinguished. Sexual maturity in males was determined on the basis of presence of spermatozoa in histological sections of testes and epididymides. A subsample of testes and epididymides was measured before fixation in 5% seawater-buffered formalin. Large testes were cut into 2 cm sections before fixation.

Samples from the periphery and the core of midsections of the testes and midsections of epididymides were taken for histological examination. The samples were embedded in paraffin, microtome-sectioned at 6 µm, then stained with haematoxylin and eosin. The sections were examined for spermatogonad activity using a transmitted-light microscope. The diameters of ten circular seminiferous and epididymal tubules were measured, and the mean of each set of measurements calculated.

Uteri were cut off at the cervix, trimmed and opened, to accomodate later examination. Ligaments were removed before preservation in 5% seawater-buffered formalin for at least two weeks. A subsample was measured before fixation. Mass of the entire uterus, and diameter and thickness of the uterus wall at mid-length, were measured. The diameter and thickness at mid-length and the total length were measured for each uterine horn. Uteri were examined for foetuses and for evidence of pregnancies. Standard length, sex and body mass of foetuses were determined. Length and mass were measured for ovaries. After fixation the ovaries were sliced by hand in 2–3 mm sections and examined for numbers and sizes of corpora lutea (CL), corpora albicantia (CA) and follicles. Terminology of female reproduction follows Perrin & Donovan (1984). The diameter of these structures was
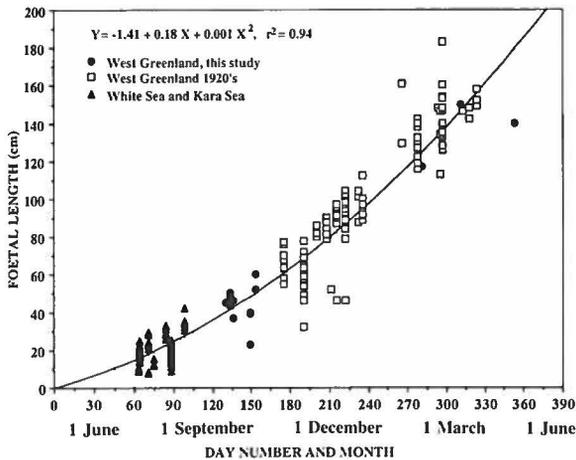
Fig. 3. Growth in length of white whale foetuses collected in West Greenland in 1985, 1989–92 (this study), in South Greenland in 1925–27 (Degerbøl & Nielsen 1930) and in the White and Kara seas between 1973 and 1984 (Ognetov 1985).

Table 3. Body mass-at-age of female and male white whales taken in West Greenland from 30 September to 4 October 1991.

Age (GLGs/2)	Females			Males		
	n	Mean mass (kg)	95% CI	n	Mean mass (kg)	95% CI
0–1	2	194	–	2	101	–
1–2	5	284	266–342	3	293	138–447
2–3	14	341	316–365	10	328	303–353
3–4	6	376	323–430	8	393	356–430
4–5	9	443	402–485	5	478	473–583
5–6	4	456	430–482	4	577	483–671
6–7	3	548	415–680	3	515	408–622
7–30	11	614	566–663	1	600	–

estimated by adding the largest and smallest diameter measured with a micrometer, then dividing the sum by two. Follicles of less than 1 mm were not measured. No attempt was made to distinguish between corpora atretica and CAs (Perrin & Donovan 1984).

Females were classified as mature if they had at least one ovarian corpus or if they were pregnant or lactating. Pregnancy was detected by the presence of a foetus. Lactation was identified by the presence of white creamy milk exuding from the nipples or mammary glands. Mature females which were neither pregnant nor lactating

and had no other signs of recent delivery or mature follicles were considered resting.

Stomach contents

Stomachs of young, dark whales were examined for milk. For older whales, samples of the stomach contents were collected. Entire stomachs were collected from nine whales from the municipality of Upernavik in October 1990 and from four whales from Qeqertarsuaq in May 1992. Subsamples of 2–3 liters of stomach contents were collected from the municipality of Upernavik (n = 21) in 1985 and 1989 and from Qeqertarsuaq (n = 2) in 1989. Otoliths, squid beaks, invertebrate skeletons and other identifiable remains were classified to the lowest possible taxonomic level.

Table 2. Length-at-age of female and male white whales from West Greenland from late September through early November and from the White and Kara seas from July through September.

| Age (GLGs/2)	West Greenland						White Sea and Kara Sea					
	Females			Males			Females			Males		
	n	Mean length (cm)	95% CI	n	Mean length (cm)	95% CI	n	Mean length (cm)	95% CI	n	Mean length (cm)	95% CI
0–1	6	212	186–238	7	186	153–219	6	197	187–207	14	191	178–205
1–2	11	251	236–266	14	251	230–272	10	225	208–243	15	237	220–254
2–3	33	277	271–283	29	274	269–280	17	268	260–276	17	271	262–280
3–4	23	303	293–312	20	302	293–311	13	301	287–314	17	311	295–328
4–5	16	312	301–322	13	318	307–328	20	306	296–316	14	309	298–319
5–6	9	327	317–337	11	341	329–353	14	319	304–334	11	332	318–345
6–7	18	349	340–358	7	372	332–412	18	342	334–350	13	357	342–371
7–8	17	349	340–358	4	421	356–486	8	350	327–372	12	369	357–381
8–9	10	355	338–372	1	385		24	354	348–360	13	380	366–395
9–10	11	363	350–375	5	436	365–506	17	358	351–366	25	378	370–387
10–11	11	368	347–388	8	444	405–483	13	361	352–370	27	395	386–404
11–12	8	369	339–398	4	456	424–488	9	371	353–389	21	397	385–408
12–13	6	375	350–401	5	461	441–480	13	369	355–383	15	400	388–412
13–14	7	383	363–403	3	463	413–514	12	368	357–379	13	412	400–424
>14	10	395	380–410	4	461	417–504	64	373	369–378	85	429	424–434
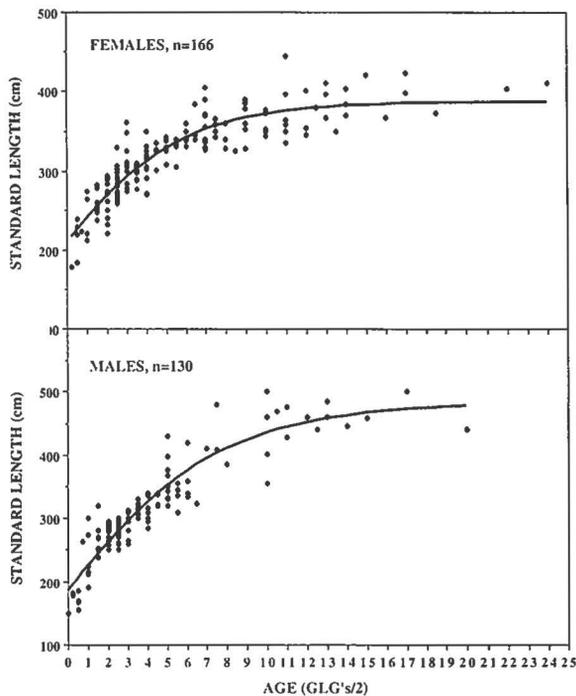
Fig. 4. Growth in length for female and male white whales from West Greenland. The curves are fitted by the Gompertz model (see Table 4 for parameters).

Results

Body growth

Foetal growth

Timing and growth in length of foetuses collected in autumn and spring (1985, 1989–92) are reasonably consistent with the foetal development described from Degerbøl & Nielsen's (1930) sample collected between 27 November and 12 April (1925–27; Fig. 3). However, the early growth of embryos is not represented in either of the two samples. To estimate the early growth we have used data from white whales taken in the White and Kara seas in July through September (1973–84; Ognetov 1985; Fig. 3). Backward extrapolation of the second-order polynomial fitted to the data from the White and Kara seas and West Greenland indicates that implantation takes place in May or early June.

The large variation in length of near-term foetuses (Degerbøl & Nielsen's and our samples) prevents exact estimation of body length and time of birth (Fig. 3). If the average length at birth is assumed to be 160 cm, then gestation apparently lasts 315 days and calves are likely to be born in mid April. However, the polynomial regression of foetal growth depicted in Fig. 3 does not account for a possible decline in growth in the last part of the foetal development. This may delay the peak of the parturitions.

That parturition can occur in May is confirmed by observations of a lactating female caught on 14 May 1992. She had a distended vulva, obvious placental scars

Table 4. Growth constants (b, k) and asymptotic length (L$_x$) and body mass (W$_x$) of female and male white whales from West Greenland and the White and Kara seas. Parameters were fitted to the Gompertz growth model and the General Growth Equation for M = 3. No convergence could be achieved for male body mass-at-age (n = 39; Fig. 5). Numbers in brackets indicate 95% confidence intervals and n indicates sample size.

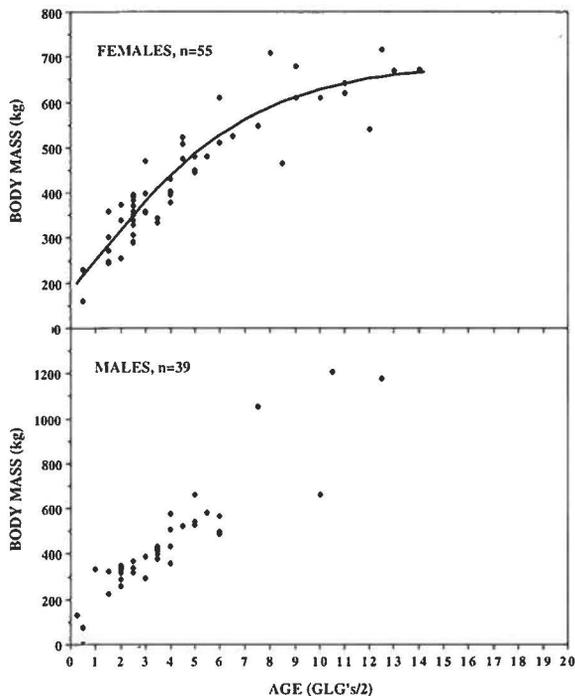| Parameter | Length-at-age (cm) | | Body mass-at-age (kg) |
	Females	Males	Females
West Greenland:			
L$_x$/W$_x$	386	483	683
	(374–398)	(458–509)	(617–748)
b	0.62	0.95	0.45
	(0.56–0.67)	(0.89–1.01)	(0.38–0.51)
k	0.27	0.22	0.27
	(0.21–0.32)	(0.18–0.26)	(0.18–0.35)
n	166	130	55
White Sea and Kara Sea:			
L$_x$/W$_x$	375	434	
	(370–379)	(427–441)	
b	0.65	0.75	
	(0.60–0.70)	(0.71–0.79)	
k	0.31	0.21	
	(0.27–0.34)	(0.19–0.23)	
n	258	312	

Fig. 5. Growth in body mass for female and male white whales from West Greenland. The curve for females is fitted by the General Growth Equation (see Table 4 for parameters). No convergence could be achieved for males. The three males exceeding 1000 kg were from May 1992 while all other males were from October 1991.

four foetuses were weighed; three from 2 October 1989 all had body masses of 2 kg with standard lengths of 43, 48 and 49 cm. One foetus from 17 October 1990 had a body mass of 300 g with a standard length of 23 cm.

Growth in length and mass of West Greenland white whales

Dorsal curvilinear lengths were 4.6% (95% CI 3.0–6.3) larger than standard lengths. Rates of growth in standard length and body mass of immature white whales are similar in both sexes (Tables 2–3). In October male and female calves could be distinguished from whales older than one year on the basis of their body length. Some of the variation in lengths of whales in age class 0–1 can be attributed to difficulties in determining their exact ages.

Both von Bertalanffy and Gompertz growth models failed to account for less than 15% of the variation in the length-at-age data, and both showed significant differences in size between the sexes (t-test, $P < 0.05$; Fig. 4 & Table 2). The residual sums of squares were marginally smaller for the von Bertalanffy model, but this model slightly over-estimated the asymptotic length of males (L_∞ = 501 cm) which also had a larger standard error. Hence the Gompertz function was chosen for the estimation of growth parameters (Table 4). Growth rates seem to be approximately equal for both sexes until about 10 GLGs. Thereafter the rate of female growth declines while the male growth rate remains high for another 10–15 GLGs (Table 2).

The General Growth Equation (M = 3) fitted to body mass at age explained 99% of the variation in female mass, whereas convergence could not be reached for males (Fig. 5). Three males killed in May 1992 had body masses of more than 1000 kg, which is 400–500 kg more than females of similar age. They suggest the likely magnitude of the asymptotic mass in males. One male of 1050 kg from May was 30% heavier than a male of

and a uterus mass (1877 g) that was intermediate between the average pregnant and the average lactating white whale (Table 8, later). She also had elevated levels of progesterone and prolactin (Høier & Heide-Jørgensen 1994). These characteristics allow us to infer that this whale had given birth recently.

Of ten foetuses with known sex, six were males. Only

Fig. 6. Asymptotic standard lengths with 95% confidence intervals for female and male white whales from various areas. Asymptotic lengths for Alaska, Hudson Bay and northern Québec were fitted by the Gompertz growth equation (Doidge 1990a).
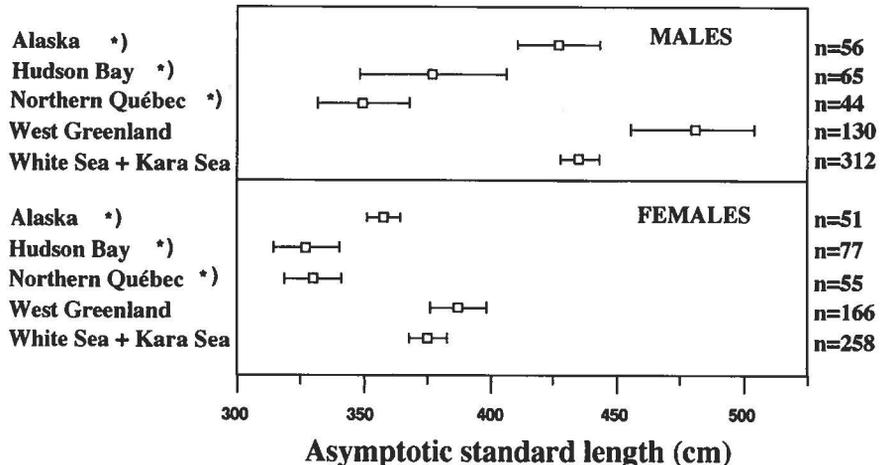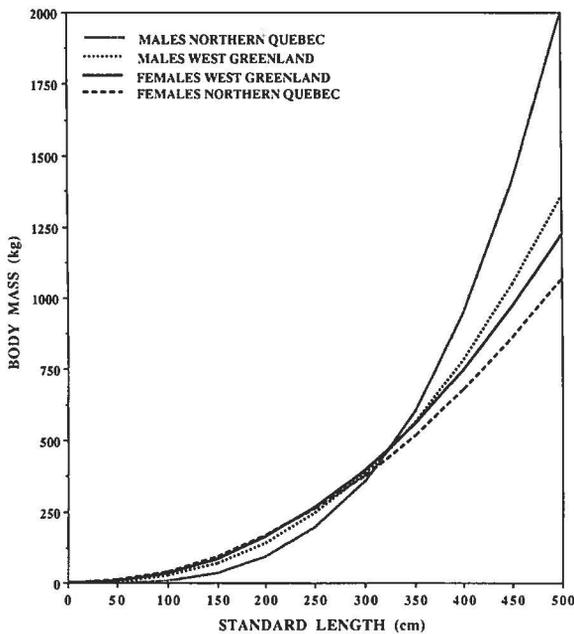
Fig. 7. Comparison of length-body mass relations between male and female white whales from two different populations: West Greenland (this study) and northern Québec (Doidge 1990a). The curve was fitted by the function: body mass = a* SL^b.

Table 5. Geometric relationship between body mass and standard length, body mass = a* SL^b. Numbers in brackets indicate 95% confidence intervals and n indicates sample size. The correlation (r^2) between body mass and SL was larger than 0.98 for all regressions. Data from northern Québec from Doidge (1990a).

| | Body mass versus length | | |
	Females	Males	Both sexes
West Greenland:			
a (x10^{-4})	13.68	2.95	5.14
b	2.21	2.47	2.37
	(2.00–2.41)	(2.29–2.65)	(2.25–2.50)
n	57	41	98
Northern Québec:			
a (x10^{-4})	35.15	0.02	0.31
b	2.03	3.37	2.85
	(1.35–2.71)	(2.68–4.10)	(2.59–3.12)
n	20	16	36

had the closest to a cubic relationship between length and body mass (b = 3.37, 95% CI 2.60–4.14), whereas the

similar age and length from October; this could perhaps indicate the magnitude of seasonal variation in body mass.

Growth in white whales from other stocks

The asymptotic length of West Greenland white whales is compared to that of white whales from other areas (Fig. 6). Greenland white whales are significantly longer (t-test) than white whales from Alaska, Hudson Bay and northern Québec (see Doidge 1990a for data on the these stocks).

To allow comparison with the samples from all other areas the Gompertz growth model was chosen for predicting growth of white whales in the White and Kara seas. White whales from these seas reached identical asymptotic lengths and hence the growth data were pooled for each sex. Male white whales from the White and Kara seas were evidently smaller than male white whales from West Greenland, and they were not significantly larger than males from Alaska (t-test, P > 0.05; Fig. 6). Female white whales from Alaska were smaller than those from the White and Kara seas (Fig. 6, P < 0.05), which were, as in males, significantly (P = 0.05) smaller than West Greenland females.

The geometric relationships between length and body mass for male and female white whales from West Greenland were compared with those for white whales from northern Québec (Fig. 7), the area with the shortest white whales (Fig. 6). Male white whales from northern Québec
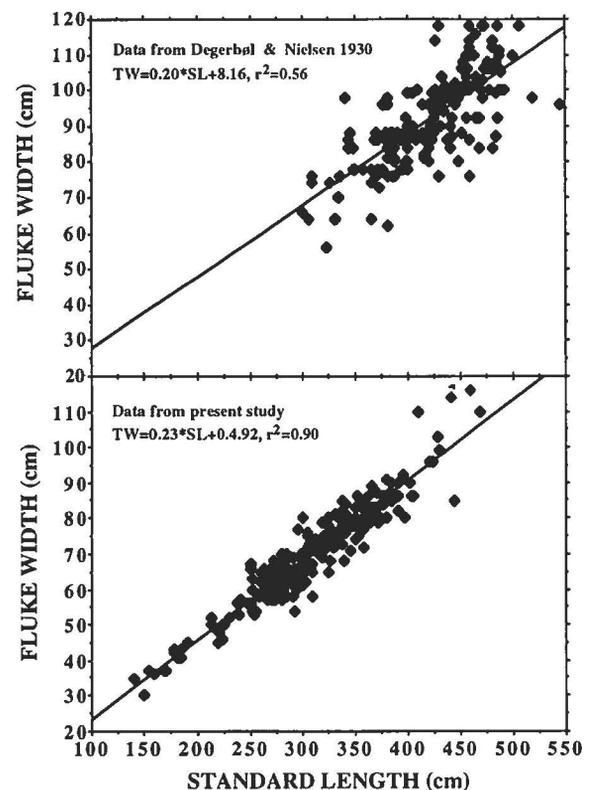

Fig. 8. Linear regressions of the width of the tail flukes (TW) on standard length for two sets of white whale samples. The uppermost figure shows measurements from the 1920s presented by Degerbøl & Nielsen (1930) from southwestern Greenland. The lower figure shows measurements from 1985–1992 from the present study.

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Table 6. Comparison of testes and epididymides measurements and histology from immature and mature white whales. Right and left testes and epididymides were mixed together and all measurements were taken on formalin-fixed tissue.

	Immature whales Mean	95% CI	n	Mature whales Mean	95% CI	n
Testes						
Mass (g)	26.0	23.7–28.3	130	540.0	453.9–626.2	24
Length (cm)	7.4	7.2–7.7	133	19.6	18.4–20.7	23
Large diameter (cm)	2.4	2.4–2.5	134	6.7	6.2–7.1	23
Small diameter (cm)	1.9	1.8–2.0	134	5.3	4.9–5.8	23
Tubuli diameter (μm)	73	57–89	4	172	163–181	21
Epididymides						
Mass (g)	39.9	35.3–42.6	124	176.4	138.5–214.4	18
Length (cm)	15.0	14.3–15.7	124	29.4	26.2–32.6	20
Large diameter (cm)	2.4	2.2–2.5	126	3.6	3.1–4.0	23
Small diameter (cm)	1.0	1.0–1.1	126	1.8	1.4–2.2	23
Tubuli diameter (μm)	–	–	0	1544	1440–1647	22

exponent b was significantly smaller than 3.00 for females in northern Québec and for females and males in West Greenland (Table 5). Insufficient sample size, with no males larger than 885 kg, probably explains the different exponent for males from northern Québec.

Correlation between fluke width and standard length

Measurements of fluke width are useful for calibrating imprecise length measurements. Standard length and width of flukes are closely correlated ($r^2 = 0.90$), except in the case of a few large males with fluke widths exceeding 100 cm (Fig. 8). In a sample of West Greenland white whales taken in the 1920s, unspecified measurements of body length and fluke width were made for 184 whales (Fig. 8; Degerbøl & Nielsen 1930). However, that sample is not directly comparable with ours because 41 body lengths exceeded the largest obtained in the present study (468 cm), and Degerbøl & Nielsen did not measure fluke widths of animals less than 300 cm long. Despite the apparently close correlation, the large animals evidently add to the variability and should be excluded when comparing the two samples. If whales with body lengths of

Table 7. Changes in size of fresh and formalin-fixed testes, epididymides, uteri and ovaries of immature and lactating white whales. Left and right organs were not distinguished and instead the letters A and B were assigned to each set of organs (testes + epididymides, uterine horn + ovary). Levels of significance for one-tailed paired t-tests are given as NS = not significant, * = significant at $0.01 < P < 0.05$, ** = significant at $0.001 < P < 0.01$, and *** = significant at $P < 0.001$.

| Organ	Immature males Change %	Signifi-cance	Organ	Immature females Change %	Signifi-cance	Lactating females Change %	Signifi-cance
Testes			*Uterus*				
Mass A	−11	*	Mass	−3	***	0	NS
Mass B	−11	NS	Length A	−6	***	−7	***
Length A	−12	***	Length B	−7	***	−8	**
Length B	−10	***	Diameter	−10	***	−8	***
Large diameter A	−4	**	Wall thickness	+46	***	+68	***
Large diameter B	−4	**					
Small diameter A	+36	**	*Uterine horn*				
Small diameter B	+25	**	Diameter A	−10	***	−14	***
			Diameter B	−11	***	−12	***
Epididymides			Wall thickness A	+50	***	+73	***
Mass A	−10	***	Wall thickness B	+65	***	+86	***
Mass B	−2	***					
Length A	−9	***	*Ovaries*				
Length B	−8	***	Mass A	−16	***	−6	**
Large diameter A	−7	NS	Mass B	−19	***	−4	*
Large diameter B	+4	NS	Length A	−15	***	−15	***
Small diameter A	+50	***	Length B	−16	***	−15	***
Small diameter B	+43	***					
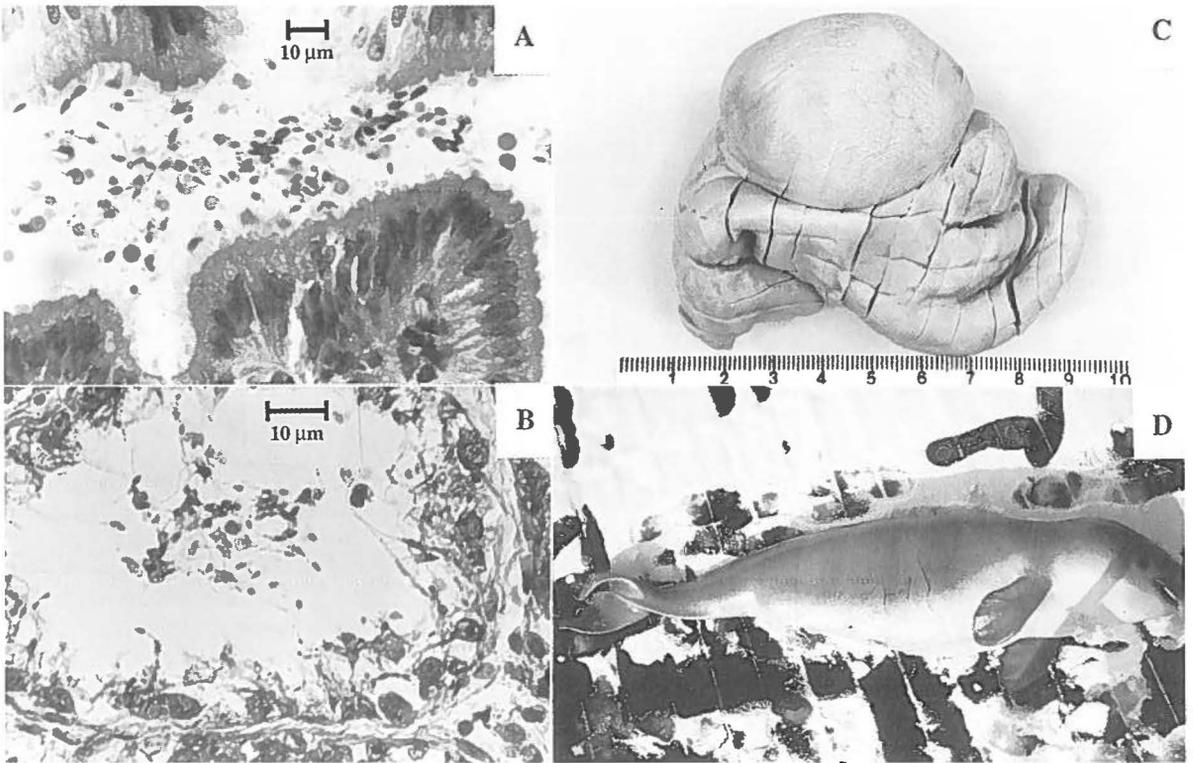
Fig. 9. Micrographs of haematoxylin- and eosin-stained sections of a) testis (x800) and b) epididymis with spermatozoa from white whales taken in May 1992. c) Ovary with corpus luteum and accessory corpora lutea from Upernavik 2 October 1989. d) Foetus (SL = 140 cm) of white whale from Qeqertarsuaq (Godhavn) 9 May 1992.

300–468 cm are compared for the two samples, the slopes and intercepts of the regressions are identical (P > 0.2), but the larger sample from Degerbøl & Nielsen (1930) shows a much greater variability, perhaps because the animals were measured less carefully.
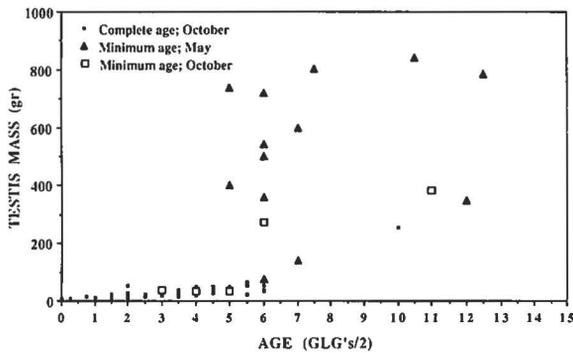

Fig. 10. Testis mass as a function of age.

Reproduction

Male reproduction

No difference in tubule diameter or presence of spermatozoa could be detected between peripheral and core samples of testes, hence peripheral sections from the plane adjacent to the epididymides were chosen for comparisons (Table 6).

Paired comparison of external measurements (mass and length) of testes and epididymides from immature whales shows that both organs shrink considerably during formalin fixation and that most measurements vary significantly between fresh and formalin-fixed tissue (Table 7). Also, the shape of both organs changes as the large diameters tend to decrease and the small diameters tend to increase. The comparison of testis size was done with formalin-preserved samples. Gonads from mature males taken in autumn and spring were significantly larger (P < 0.05) in all respects than those from immature whales (Table 6). Any external measurement of testis can therefore be taken as diagnostic for sexual maturity.

In spring (April-May), testes (and epididymides) taken from mature males were significantly larger (P < 0.05) in

Table 8. Comparison of uterus and ovary measurements from immature, lactating/resting and pregnant white whales from October. Right and left organs were mixed together and all measurements were taken on formalin-fixed tissue.

	Immature whales			Lactating or resting whales			Pregnant whales		
	Mean	95% CI	n	Mean	95% CI	n	Mean	95% CI	n
Uterus									
Mass (g)	190	158–221	82	1045	869–1222	26	3502	3043–3961	9
Length A (cm)	27	25–28	82	44	41–48	26	64	54–74	9
Length B (cm)	28	26–29	79	46	42–49	26	66	50–83	8
Diameter (cm)	4.7	4.4–5.1	83	10.0	8.9–11.1	26	23	18–28	8
Wall thickness (mm)	5.5	5.0–6.0	83	9.7	8.2–11.1	26	7.4	5.5–9.3	9
Diameter of horn A (cm)	4.0	3.7–4.3	83	8.6	7.8–9.4	26	31	21–42	6
Diameter of horn B (cm)	4.1	3.8–4.3	83	9.0	8.1–10.0	26	34	20–48	5
Thickness of horn A (mm)	4.2	3.8–4.4	81	7.8	6.6–9.0	26	4.7	2.5–6.9	9
Thickness of horn B (mm)	4.4	4.0–4.8	82	7.8	6.6–9.0	26	5.3	3.4–7.2	8
Ovaries									
Mass A (g)	14	12–15	82	40	35–46	25	79	64–95	9
Mass B (g)	14	13–15	81	43	38–48	24	57	38–76	10
Length A (cm)	6.5	6.3–6.8	83	8.5	7.9–9.2	26	9.5	8.0–11.0	8
Length B (cm)	6.7	6.5–7.0	78	8.9	8.3–9.6	24	8.8	7.9–9.6	10

length and mass than those sampled in autumn (September-October) (Fig. 10). Spermatozoa could be detected in samples from both October and May, but they were subjectively assessed to be more abundant in samples from May (Fig. 9). The autumn samples of testes with spermatozoa had no spermatozoa in the epididymides (n = 2).

All mature males, except one, had worn teeth with no neonatal line. As a result, age at sexual maturity is underestimated. Males younger than 6 years were all sexually immature. Two animals which were at least 6 years old were sexually mature. Seven of eight and three of four immature whales of 5 and 6 years, respectively, had no tooth wear (complete age; Fig. 10). Males probably reach sexual maturity at an age of 6–7 years.

No males shorter than 380 cm were sexually mature and all longer than 400 cm were mature.
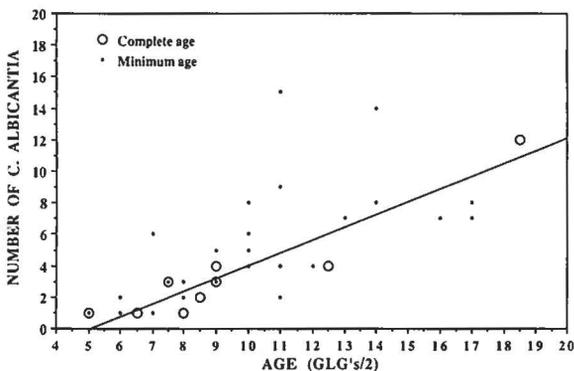

Fig. 11. Relationship between the total number of corpora albicantia and the age of 34 white whales.

Female reproduction

The uterus and ovaries show deformations during formalin fixation similar to those described for male sex organs. Generally the organs shrink during fixation, except that the thickness of the uterine walls increases significantly (Table 7).

The majority of females were collected during the autumn, a time when mature females either carry a foetus, have a suckling calf, are resting or have recently aborted. All females classified as sexually mature carried either a CL or a CA or were lactating.

One CL from a pregnant female taken in March had a diameter of 48 mm, and the mean of the diameters of 10 CLs from pregnant white whales taken in October was 41 mm (95% CI 39–44 mm). Three of the latter had accessory CLs on the same ovary, but these were considerably smaller than the primary corpora. One lactating white whale without a foetus taken in October had a small, but characteristic CL (14 mm), well below the mean size of CLs in October. This female may have aborted an earlier pregnancy.

The mean of the diameters of the largest CAs measured from 23 lactating white whales in October was 14 mm (95% CI 13–15). This value was not statistically different from the diameters of the largest CAs in five pregnant whales (mean = 14.95% CI 10–18) or from those in three lactating and pregnant whales (mean = 13.95% CI 5–21). The largest number of CAs in one ovary was 8; in both ovaries combined the largest number was 15. Regression of the number of CAs on age of whales with complete age suggests an age at first parturition of 5 years and an accumulation of 0.8 CAs per year ($r^2 = 0.89$; Fig. 11). The annual accumulation of CAs exceeds the pregnancy rate (see below), probably because accessory CLs or lutei-

Table 9. Reproductive status in relation to age for female white whales from West Greenland. All except two lactating females (8 and 12 years old) were taken in October. Parentheses indicate the subset of whales where the indicated age is minimum age because no neonatal line was detected in tooth sections (see Heide-Jørgensen et al. 1994).

Age (GLGs/2)	Number of animals in different reproductive categories						
	Imma-ture	Mature	Preg-nant	Lacta-ting	Pregnant & lactating	Resting	Sum
1–2	9						9
2–3	32						32
3–4	21						21
4–5	14(1)	1					15
5–6	6	2(1)		1		1(1)	8
6–7	2	5(4)	1(1)	4(3)			7
7–8	1(1)	9(6)	2(2)	5(3)	1(1)	1	10
8–9		4(2)	2(1)	2(1)			4
9–10		5(4)		5(4)			5
10–11		5(3)	1	2(2)	2(1)		5
11–12		5(5)	1(1)	4(4)			5
12–13		4(1)		4(1)			4
13–14		1(1)		1(1)			1
14–15		3(1)		1(1)	1(1)	1(1)	3
+15		6(4)		5(4)	1(1)		6
Sum	85	50	7	34	5	3	135

nized follicles sometimes give rise to several CAs (see Brodie 1971, Sergeant 1973).

The largest follicles in ovaries from 31 mature white whales taken in October had a mean diameter of 4.3 mm (95% CI 3.3–5.7 mm), whereas four whales taken in March-May had follicles with a mean of 7.5 mm (95% CI 2.7–12.3 mm). Examination of females in October showed that the mean length of nipples was about 2.0 cm (95% CI 1.9–2.2 cm) for 17 lactating whales, and less than 0.5 cm for four non-lactating.

The oldest immature female had a minimum age of 7 years. Most other immature whales had neonatal lines and their ages can be considered complete (Table 9). One pregnant female of 6 years or more had no CAs and therefore is assumed to have been pregnant for the first time. Another pregnant female with a complete age of 8
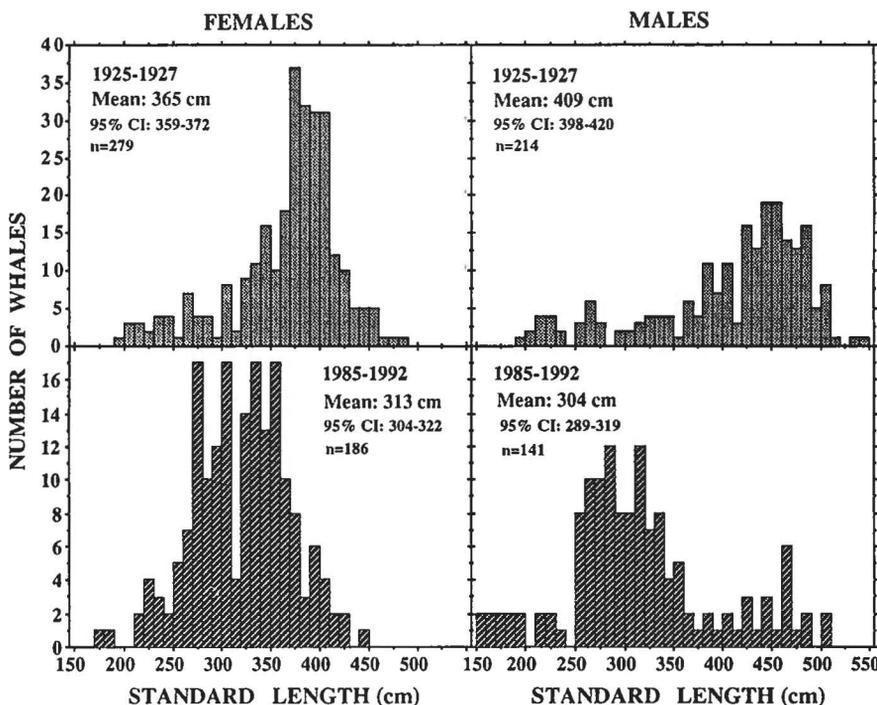

Fig. 12. Length distribution of landed white whales in two samples from West Greenland. The uppermost figures show the measurements from the 1920s presented by Degerbøl & Nielsen (1930) from southwestern Greenland. The lower figures show measurements from 1985–1992 from Disko Bugt and Upernavik.

FEMALES

1925-1927
Mean: 365 cm
95% CI: 359-372
n=279

1985-1992
Mean: 313 cm
95% CI: 304-322
n=186

MALES

1925-1927
Mean: 409 cm
95% CI: 398-420
n=214

1985-1992
Mean: 304 cm
95% CI: 289-319
n=141

STANDARD LENGTH (cm)

NUMBER OF WHALES

Fig. 13. Age distribution of male and female white whales caught in the drive fishery in Upernavik 1985, 1989–1991 and in Disko Bugt 1990–1992.
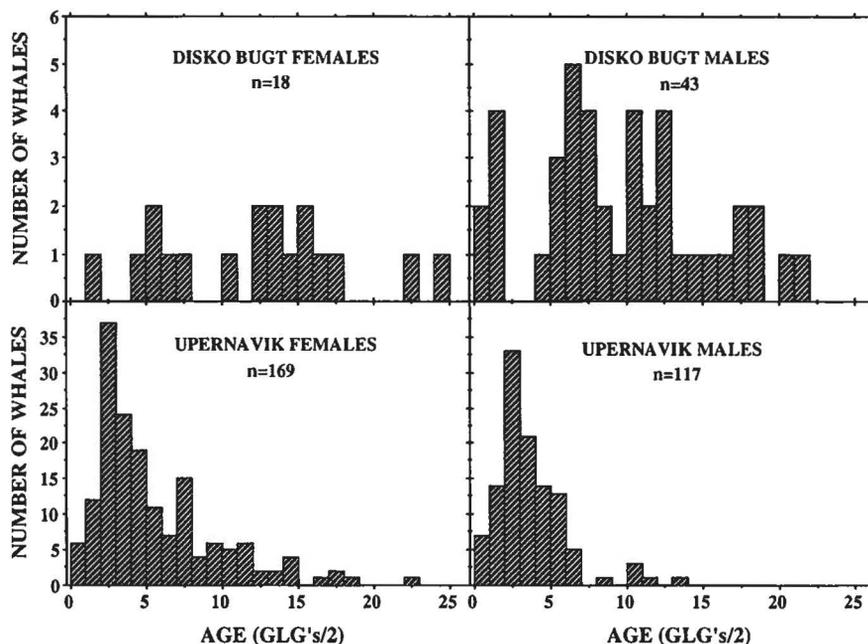
years had 1 CA. She would at the earliest have become pregnant for the first time at 5 years if birth intervals of 3 years are assumed. Two lactating females of complete ages of 5 and 6 years each had 1 CA, suggesting that they had become pregnant for the first time at ages of 4 and 5 years, respectively, or possibly 3 and 4 years if lactation lasts two years. However, other whales with complete ages had numbers of CAs that would, on the assumption of a three-year birth interval, give widely varying estimates of age at first pregnancy (Fig. 11). Despite the difficulties of estimating the age at first ovulation or first pregnancy, most first pregnancies apparently occur at ages of 4–7.

The two longest immature females were 340 and 348 cm in SL (6 and 3 years old, respectively). The shortest pregnant female was 327 cm (7 years) and the shortest lactating female was 325 cm (5 years). The length at which 50% of the females were mature was 345 cm.

Not all whales were checked for both lactation and pregnancy. However, among 25 lactating whales found to be non-pregnant, at least one pregnant whale was not lactating, and four whales were both pregnant and lactating. The pregnancy rate of 0.31 is calculated as the ratio between the number of pregnant whales (n = 11; Table 9) and the total number of mature whales examined for pregnancy (n = 36; Table 11, later).

Age, length and sex distributions in catches

Degerbøl & Nielsen (1930) could not estimate ages for their sample of white whales taken in 1925–1927, so comparisons with the present sample must be made on the basis of length distributions (Fig. 12). It is obvious that there was some size and sex selectivity in the drive-net fishery in the 1920s, as there has been in the recent harvesting. Young whales were obviously under-represented in the catch in the 1920s or they were not measured as consistently by Degerbøl & Nielsen as in this study (Fig. 12). We attempted to measure all landed whales but our sample, for unknown reasons, also shows a deficiency in length classes shorter than 250 cm (Fig. 12). Nevertheless, the whales from the 1925–27 sample were significantly (P < 0.05) longer for both sexes, even when both samples are truncated at 300 cm to avoid the bias caused by under-representation of young whales. Although the whales landed in the 1920s were generally longer than those harvested in recent years, they were not unrealistically long compared to recent measurements. The longest female and male from 1925–27 were 482 and 545 cm, respectively, compared with 444 and 500 cm for the present study.

The age and length distributions show clear differences between the autumn samples from the municipality of Upernavik and the spring samples from Disko Bugt (Fig. 13). Only seven males from Upernavik exceeded the minimum length (SL = 380 cm) at sexual maturity, whereas 48 females exceeded the minimum length at sexual maturity (SL = 345). For the spring samples from

Table 10. Prey items of white whales from West Greenland waters illustrated by presence of otoliths and squid beaks (divided by two) and other hard remains retrieved from subsamples (ss) of stomach contents or entire stomachs (es), range given in brackets. + indicates presence of squid beaks.

Area and year sample/ (GLGs/2)	A. glacialis or B. saida	S. marinus	Lantern-fish	Hali-but	Squid	Crustacean
Upernavik 1985, 1989						
Mean number in 9 es (0.75–10)	211 (45–730)	0	9 (0–20)	0.1 (0–1)	+ (1–27)	*Pasiphaeidae* sp., *Hypenidae* sp., *Pandalus* sp.
Mean number in 21 ss (1–10)	71 (12–285)	0	2 (0–10)	0	+ in 30%	*P. borealis*, *Pasiphaeidae* sp. *Pandalus* sp.
Qeqertarsuaq 1989–90, 1992						
Mean number in 4 es (7.5–12.5)	0.3 (0–1)	8 (1–25)	0	0.3 (0–1)	+ (> 200 in all)	*P. borealis*
Mean number in 2 ss (6–7.5)	0.5 (0–1)	4 (2–5)	0	0	+ in 50%	*Pandalus* sp.

Disko Bugt, 18 males and 6 females exceeded the minimum length at sexual maturity.

The samples from Disko Bugt represent a longer period of the year (February-May) and a wider array of hunting situations (ice edge, ice entrapment, open water) than do the samples from the municipality of Upernavik. The latter are all from the drive fishery in October. The sample size is too small for Disko Bugt samples to be considered representative of the variety of hunting situations involved. The samples nevertheless show that there is sex and age segregation of white whales in the two areas. Few mature males were taken in the municipality of Upernavik, and the herds exploited there clearly consisted of mainly mature and immature females and immature males (Fig. 13). Mature males are, however, found in the samples from Disko Bugt.

Feeding habits

One whale taken in late September with zero GLGs and a SL of 155 cm had nothing but milk in its stomach. This animal presumably was a calf of the year. Two other whales taken at the same season had one (SL = 219 cm) and two (SL = 215 cm) GLGs and are assumed to have been born in the previous year. Both had a mixture of milk, fish remains and squid eyes in their stomachs. Several whales with 2–4 GLGs had remains from fish and squid in their stomachs.

Due to decomposition of samples of stomach contents, it was generally impossible to distinguish between polar cod (*Boreogadus saida*) and arctic cod (*Arctogadus glacialis*). However, among those otoliths that could be identified *B. saida* was by far the most numerous of the

two species. Although estimation of their relative quantitative importance was not attempted, the two cod species clearly contributed more to the white whale diet than any other prey item in the Upernavik area. Squid beaks were also numerous in white whale stomachs from both Upernavik and Disko Bugt. Redfish (*Sebastes marinus*), dominated in the samples from Disko Bugt. Halibut (*Reinhardtius hippoglossoides*) and shrimp (*Pandalus borealis*) were found infrequently in stomachs from both Upernavik and Disko Bugt, but lanternfish (Myctophidae) were found only in stomachs from Upernavik (Table 10).

Discussion

Body growth

Complete age can only be derived for age classes younger than 14 GLGs for males and younger than 20 GLGs for females (Heide-Jørgensen *et al.* 1994). This limitation adds to the uncertainty of estimates of age at sexual maturity, age-specific mortality and growth increment in relation to age. Growth curves in particular will be biased to the left because of truncation due to the incomplete age determinations. Hence the overall growth is accelerated when using minimum ages, *i.e.* underestimating age, and the theoretical age at physical maturity may therefore be attained earlier than in reality. This bias is especially pronounced in males where the neonatal line becomes worn away (at approximately 14 GLGs) earlier than in females (at approximately 20 GLGs) (Heide-Jørgensen *et al.* 1994).

However, for comparative purposes it can be assumed that this uncertainty is uniformly distributed across populations and that, for instance, asymptotic growth has similar errors from incomplete ages in different populations.

The sexual dimorphism described for other white whale stocks (see Doidge 1990a; Stewart 1994) is also evident for West Greenland white whales with respect to length. Body mass is subject to seasonal variations which remain to be quantitatively assessed for West Greenland white whales. However, Degerbøl & Nielsen (1930) mentioned that the white whales had thin blubber layers when they arrived in southwestern Greenland in November and were fatter in April when they left the wintering grounds.

The maximum length of white whales taken in the drive-net fishery in southwestern Greenland during the 1920s exceeded the maximum length of white whales measured in any other North Atlantic population, including the one that is currently exploited in West Greenland. Vladykov (1943) and Doidge (1990a) suggested that the exceptional lengths reported by Degerbøl & Nielsen were curvilinear rather than SLs. Curvilinear length exceeds SL by less than 5%; thus not all of the difference can be explained as an artifact of different measuring procedures. The width of the tail flukes is a less ambiguous measurement than SL, and the 1920s fluke measurements are greater than recent Greenland measurements.

If measurement error is ruled out as the explanation for the exceptionally large whales in Degerbøl & Nielsen's sample, two alternative hypotheses could explain the disparity between current and previous length distributions of white whales from West Greenland:

1. As a consequence of heavy exploitation in West Greenland throughout this century, the age structure has changed and old, large white whales are either rare or absent in the population.

2. Better (e.g. more abundant, more nutritious) prey may have been available to white whales in the 1920s than now. This would account for the larger size at physical maturity of the animals from southwestern Greenland.

These two hypotheses are not mutually exclusive. For example, a change in prey resources could in conjunction with exploitation have affected the age distribution. The increase in sea temperature in southwestern Greenland in the 1920s, and the concomitant increase in abundance of Atlantic cod (Gadus morhua) and other potential prey items (see below), may have enhanced growth potential of individual whales.

It seems unlikely that a large, genetically discrete white whale population would have occurred earlier in this century a few hundred kilometers south of the centre of the current distribution in West Greenland, and that the whales in such a population would have had a longer asymptotic SL than those in the current population. A possible connection between the southwestern Greenland, southeastern Baffin Island and northern Labrador populations, as suggested by Heide-Jørgensen (1994), would not explain the larger body size of white whales in southwestern Greenland, because these adjacent stocks off eastern Canada consist of whales that are significantly smaller than Greenland white whales (Brodie 1971, Doidge 1990a, Stewart 1994).

Reproduction

Sergeant (1973) found that sperm production began at a testis mass greater than 200 g, corresponding to a body length of 290–330 cm and an age of 7–9 years for western Hudson Bay white whales. West Greenland white whales also begin sperm production at a testis mass of 200 g or more, but such a testis size is attained at a greater body length (332–412) and an earlier age (6–7 years).

In Alaska Burns & Seaman (1986) found few or no spermatozoa in the testes and epididymides of mature males taken in April-May, whereas two males taken in mid-June had moderate numbers of sperm. They concluded that some "males may remain in breeding condition through June" but that most are in the retrogression phase by late April-May. Matings have not been reported from Greenland, but the abundance of spermatozoa detected in May samples suggests that matings occur in spring.

The lengths of three white whale foetuses from the White and Kara seas from October (45.6 cm) and December (85 and 90 cm) were identical to those of similar-aged foetuses from West Greenland (Ognetov 1985). Thus it seems reasonable to include data on growth of embryos and early foetuses from the White and Kara seas when predicting foetal development of West Greenland white whales. Measurements of foetuses from the White and Kara seas and West Greenland suggest implantation in May-June and parturition in April-May.

Parturition has been observed twice in West Greenland in April (1919 and 1923). One of the neonates reportedly was only 116 cm long. However, on this occasion the birth may have been provoked by the method of hunting the whales. Three free-swimming white whales 120, 147 and 165 cm long were measured in the last half of March 1926; judging from their lengths they must have been neonates (Degerbøl & Nielsen 1930). Heide-Jørgensen et al. (1993) observed neonatal white whales during aerial surveys off West Greenland in late March and early April. These authors were convinced from the size and colour of the calves, compared with those of accompanying adults, that the calves had been born in March of the same year. If this supposition was correct, then the period of parturition extends at least from March until May. Sergeant (1973) noted the difficulty of trying to specify the exact period of births despite the clear growth pattern of small foetuses. This difficulty was also noted by Burns & Seaman (1986) for white whales in Alaska where they estimated the birth period to extend "from April through July and perhaps later". The decline in foetal growth in

Table 11. Comparison of life history parameters from different populations of white whales. Pregnancy rate is calculated as the ratio of pregnant females to all mature females.

Parameter/Area Reference	West Greenland a)	Northern Quebec b)	Cumberland Sound c)	Hudson Bay d)	Alaska e)	White & Kara Sea f)	Sea of Okhotsk g)
Length at birth (cm)	150–160	–	160	151	155	160	170
Length of gestation (days)	330	390	441	425	441	330	345
Period of implantation	May	early May	May	mid April	mid April	May-June	April-May
Period of births	April-May	late May	August	early August	April-July	June-July	March-July
Length at sexual maturity							
Females (cm)	345	290	285	270	310	350	379
Males (cm)	390	–	384	310	–	–	415
Length at physical maturity							
Females (cm)	386	330	362	328	359	375	390
Males (cm)	483	349	427	377	427	434	–
Age at sexual maturity							
Females (GLGs/2)	4–7	6	5	4–6	4–7	2–9	–
Males (GLGs/2)	6–7	–	8	8–9	–	–	–
Pregnancy rate	0.31	0.26–0.41	–	0.47	0.34	0.36	0.33
Sample size	36	76	–	62	179	246	42

a) This study, b) Doidge 1990b and 1990c, c) Brodie 1971, d) Sergeant 1973 and Doidge 1990b, e) Burns & Seaman 1986, f) Ognetov 1981, Ognetov 1985 and this study, g) Kleinenberg et al. 1969.

the last trimester of pregnancy probably explains this extended parturition period in Alaska (Burns & Seaman 1986: fig. 14). However, few white whales are seen or caught in West Greenland between mid-May and September and we were therefore unable to describe the late phase of pregnancy in white whales.

West Greenland white whales are assumed to summer mainly in the Lancaster Sound region. Despite numerous field studies of white whales in the Lancaster Sound region during July-August, no births have been reported. White whales and narwhals classified as neonates were frequently observed on aerial surveys in Lancaster Sound in late May and early June, respectively (Cosens & Dueck 1990).

The frequency of accessory CLs for pregnant white whales from West Greenland (25%, n = 12) was higher than what has been reported from Alaska in a much larger sample (21%, n = 110, Burns & Seaman 1986), from Hudson Bay (12%, n = 44, Sergeant 1973) and from Cumberland Sound (13%, n = 39, Brodie 1971) as well as for narwhals *Monodon monoceros* (12%, n = 43, Hay 1984). However, the frequency of accessory CLs may be influenced by the time of sampling and the age composition of the sample. They may regress during pregnancy, and primiparous whales may carry accessory CLs relatively frequently as has been described for narwhals (Hay 1984).

tain both milk and solid food remains during the second year of life (Brodie 1971, Sergeant 1973, Burns & Seaman 1986).

The stomach contents of white whales taken in the municipality of Upernavik confirm that these whales consume pelagic gadids (*B. saida* and *A. glacialis*) which are also the key prey of several other species of marine mammal that summer in the high arctic, e.g. narwhals, ringed seals (*Phoca hispida*) and harp seals (*Phoca groenlandica*) (Finley & Gibb 1982, Bradstreet & Finley 1983, Finley et al. 1990, Siegstad 1988). On their wintering grounds in Disko Bugt, white whales consume several demersal and bathypelagic fish species of Atlantic origin (e.g. *Sebastes* sp. and *Reinhardtius hippoglossoides*). Redfish (*Sebastes* sp.) are also an important prey for ringed seals in Disko Bugt (Siegstad 1988). Capelin (*Mallotus villosus*), which are important prey of Hudson Bay and White Sea white whales (Sergeant 1973, Ognetov 1990), have not been found in the samples from Disko Bugt where capelin occur in large shoals during summer (Sørensen 1985). Capelin are rare north of the municipality of Uummannaq (Sørensen 1985) and it is not surprising that they were not found in white whales from the Upernavik area.

Degerbøl & Nielsen (1930) reported after examining "several hundred stomachs" that white whales in southwestern Greenland preyed exclusively on Atlantic cod, redfish, halibut and small catfish (*Anarhichas* sp.).

Feeding habits

Young white whales begin feeding on fish and invertebrates after the first year, but their stomachs may con-

Comparison with other populations

For several reasons, detailed statistical comparisons of life-history values among different white whale popu-

lations are difficult. The variability of results reported by various authors is likely due to the difficulties of tooth wear, accessory corpora and complicated field conditions that impede consistent data collection (*e.g.* detection of both pregnancy and lactation or detection of milk in stomachs). Also, the populations are subjected to different harvesting regimes, and the studies used for comparisons have been conducted over a long time span.

The population of white whales off West Greenland resembles other white whale populations in several ways. Sexual maturity, defined as first ovulation, is attained at about 85% of length at physical maturity in all white whale populations. This conforms with Laws' rule that female sexual maturity is attained at about 87% of the length at physical maturity (Laws 1956). Also, this length is attained at about the same age (6 GLGs) by females in all populations (Table 11). The pregnancy rate of West Greenland white whales indicates that about a third of all mature females are pregnant at any given instant as also found in other white whale populations (references in Table 11) and in the narwhal (Hay 1984). Hence a three-year calving interval is suggested for white whales in all areas studied (except possibly Hudson Bay).

White whales off West Greenland differ from those in other areas by their larger size at physical maturity and their apparently faster foetal growth (Fig. 6 and Table 11). All evidence suggests that white whales off West Greenland have a gestation period of less than a year, which implies that they have a more rapid foetal development than that described for white whales from Canada and Alaska (Table 11) and for narwhals (467 days, Hay 1984). However, foetal growth deserves closer examination in all white whale populations.

Acknowledgements

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