

Size-at-age relationships as discriminators of white whale (*Delphinapterus leucas*) stocks in the eastern Canadian Arctic

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White whales harvested by Inuit at Arviat on western Hudson Bay, Pangnirtung on Cumberland Sound and Grise Fiord on the north side of Jones Sound were sampled for analysis of size and age in 1984–87. The sampling sites are thought to represent western Hudson Bay, Southeast Baffin and High Arctic stocks of white whales, respectively. Males were longer than females at all locations. White whales from western Hudson Bay were significantly shorter as adults than white whales from the other two locations. Analysis of published data showed that eastern Hudson Bay white whales are also significantly smaller than Cumberland Sound whales. Differences in asymptotic length between whales from Cumberland Sound and Jones Sound, and between whales from eastern and western Hudson Bay, were not significant.

Key words:

White whale, beluga, *Delphinapterus leucas*, stocks, growth.

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Introduction

Somatic growth is a fundamental characteristic of living things. It represents a significant energy requirement and is a key correlate of a variety of lifehistory traits (Calder 1982). Examination of growth rates can provide insights into ecological interactions, such as food availability (Innes *et al.* 1981). Moreover, because growth represents the interplay between the environment and genotype, it may be useful in identifying management stocks or populations. Klumov (1937, cited in Sergeant & Brodie 1969a), Sergeant & Brodie (1969a), Finley *et al.* (1982), Stewart & Walker (1987) and Doidge (1990a) examined white whales (*Delphinapterus leucas*) from different areas to assess the usefulness of size-at-age to distinguish among putative stocks. These studies disagreed on the degree to which size-at-age can separate individuals from different stocks.

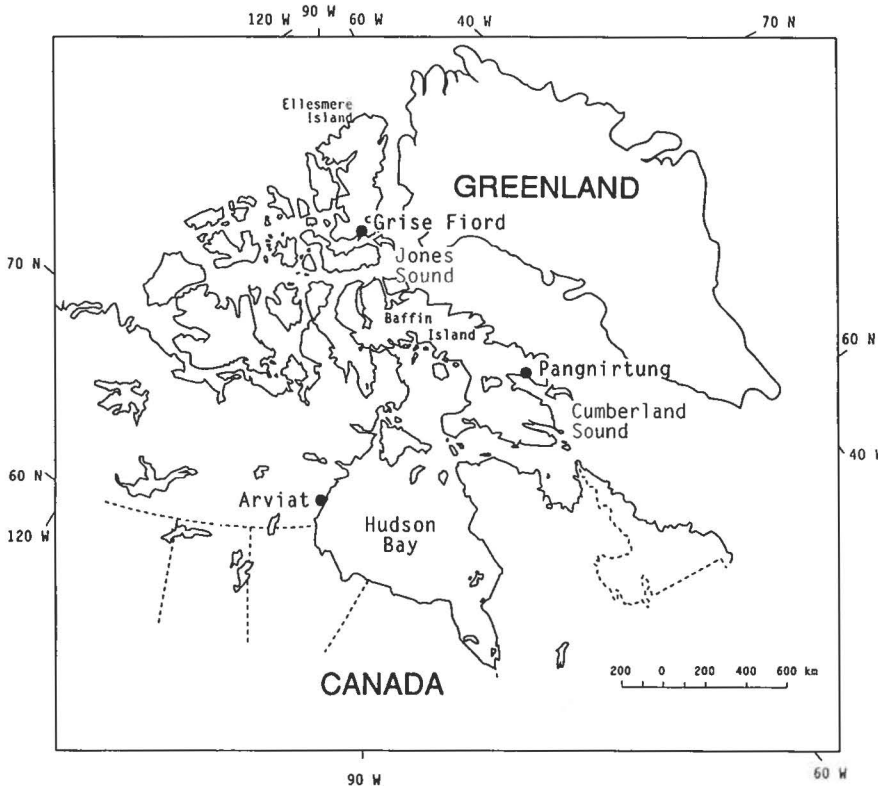
Sergeant & Brodie (1969a) reported differences in the lengths of adult male white whales between western Hudson Bay (~350 cm) and Cumberland Sound (~450 cm). Finley *et al.* (1982) were unable to distinguish among

whales sampled in eastern Hudson Bay, Ungava Bay and Hudson Strait using body length. Stewart & Walker (1987), in a preliminary analysis, concluded that whales from western Hudson Bay could be separated from whales from Cumberland and Jones sounds on the basis of growth curves. Doidge (1990a) found that while white whales from Hudson Bay tended to be shorter than others examined, differences were too slight to classify individuals on the basis of size. Here I describe growth and examine size-at-age for white whales in the eastern Canadian Arctic to distinguish among putative stocks.

Materials and methods

White whales harvested by Inuit hunters were sampled at Arviat (known then as Eskimo Point 61°05'N, 94°06'W) on western Hudson Bay, Pangnirtung (66°07'N, 65°43'W) on Cumberland Sound and Grise Fiord (76°25'N, 82°52'W) on Jones Sound, Northwest Territories (N.W.T.), Canada (Fig. 1) from 1984 to 1987 (to 1986 in Pangnirtung). These sampling sites represent the pre-

Fig. 1. Sampling locations.



sumed western Hudson Bay, Southeast Baffin and High Arctic stocks respectively (Clarke *et al.* 1989, Cosens *et al.* 1990, Richard *et al.* 1990, Bodaly *et al.* 1992). Sampling effort was concentrated on the peak hunting periods at each location: July, August and September, respectively. Whales were usually shot although hunters at Arviat also used nets.

Body mass was determined by weighing intact whales suspended from a tripod. Mass was recorded to the nearest 5 kg, uncorrected for blood loss. Linear measurements, which were made to the nearest centimeter with a steel tape measure, followed American Society of Mammalogists Committee on Marine Mammals (1961) guidelines and included: standard length and girths at the eye, axilla, navel, anus and caudal peduncle at the base of the flukes.

Both jaws were collected to provide material for age estimation. Teeth were removed after gentle boiling. Longitudinal sections, 0.3 to 0.4 mm thick, were prepared (Wainwright & Walker 1988) and stored in a mixture of equal parts of glycerine, ethanol and water (Pueck & Lowe 1975). Age estimates were obtained by counting dentinal annuli in the second or fifth mandibular tooth, viewed wet with oblique reflected light using a variablepower dissecting microscope. Each section was read three to five times. Three identical readings were accepted as the final growth layer group (GLG) count. If there were not three identical readings, the mean and the

maximum normed residual (MNR, Snedecor & Cochran 1980) was calculated for all five readings and any outliers were deleted. The final GLG count was the median of the remaining values (Stewart & Lavigne 1979). Ages were estimated by assuming that two GLGs were deposited each year (Sergeant 1973, Goren *et al.* 1987). Ages are therefore reported with half-year precision, indicating whether the last GLG formed was an odd or an even number. Absence of a neonatal line was used to determine if GLGs had been lost to tooth wear.

Gompertz growth curves for standard length and mass were fitted to the data using the non-linear curve fitting program in SAS (SAS Institute Inc. 1985). The growth curves were of the form:

$$\text{Size} = A(e^{(-e^{-k \cdot \text{age} + k \cdot t_0})})$$

where Size is length (cm) or mass (kg), A is the asymptote (cm or kg), k and t_0 are fitted constants, e is the base of natural logarithms (approximately 2.7183) and age is the estimated age of the whale (yrs). Preliminary analysis which included von Bertalanffy growth curves indicated that the Gompertz equation fit more of the data sets and produced higher F values.

The small sample sizes and the age distributions of whales from Pagnirtung and Grise Fiord precluded comprehensive comparison of the growth curves. Differences were assessed by comparing asymptotic size and by ex-

Table 1. Descriptive statistics of length (cm), mass (kg) and age (yr) for white whales sampled at three locations in the eastern Canadian Arctic.

Sex	Parameter	Location		
		Arviat	Pangnirtung	Grise Fiord
Female	length ($\bar{x} \pm 1$ SE)	283.5 \pm 7.8	337.6 \pm 22.2	321.3 \pm 15.3
	N	51	7	12
	range	129–385	241–395	254–424
	mass ($\bar{x} \pm 1$ SE)	363.7 \pm 20.1	575.7 \pm 62.7	525.5 \pm 73.9
	N	51	7	11
	range	45–685	320–840	300–1200
Male	age ($\bar{x} \pm 1$ SE)	8.3 \pm 0.9	8.5 \pm 2.2	5.6 \pm 1.6
	N	52	7	12
	range	0.0–26.0	2.5–17.0	1.5–21.0
	length ($\bar{x} \pm 1$ SE)	333.1 \pm 7.7	368.7 \pm 9.8	345.2 \pm 15.9
	N	68	25	18
	range	183–419	272–445	231–481
Female	mass ($\bar{x} \pm 1$ SE)	528.3 \pm 25.8	812.4 \pm 56.2	665.3 \pm 76.8
	N	68	25	18
	range	145–1005	385–1300	250–1630
	age ($\bar{x} \pm 1$ SE)	11.5 \pm 0.8	7.0 \pm 0.6	5.2 \pm 0.6
	N	70	25	18
	range	0.0–24.5	3.0–16.0	1.0–13.5

examining the distribution of the individual deviations around one growth curve. Asymptotes were compared using a t-test for unequal sample sizes and unequal variances (Snedecor & Cochran 1967) for sex differences at a site ($P < 0.05$) and between sites for each sex ($P < 0.01$). Asymptotes for whales from Hudson Bay (Doidge 1990a) and Alaska (Burns & Seaman 1985) were compared similarly.

Growth curves fitted to the Arviat data were used to predict size for whales from the other sites. This predicted value was subtracted from the observed value and the resulting deviations compared to the residuals of the Arviat growth curve. These data were analysed using a Kruskal-Wallis oneway ANOVA followed by Dunn's test

for unequal sample sizes (Kuo *et al.* 1992) using SigmaStat™ (Bagdasian *et al.* 1992).

Mass-length relationships were examined using log-transformed data. Differences in sampling dates among locations may have caused the mass-length relationships to vary and data were analysed separately, by sex, for each location. Mass was also examined as a function of length plus the girths at the eye, axilla, navel, anus or caudal peduncle using stepwise regressions (SAS 1985, MAXR procedure). Length was forced as the first variable and each girth was added to the stepwise regression only if it had a partial $P < 0.01$. The girths at the eye, anus and tail never achieved this limit so the equations are of the form:

Table 2. Parameters (± 1 SE) for the Gompertz equation $A(e^{-(e^{-k} \text{age} + k)})$ for length and mass of white whales from three locations in the eastern Canadian Arctic. R^2 is corrected for the mean (1-(error SS/corrected total)).

Location	Sex	Length (cm)				Mass (kg)			
		A	k (yr ⁻¹)	t_0 (yr)	R^2	A	k	t_0	R^2
Arviat	F	330.9 ± 5.2	0.31 ± 0.04	-0.96 ± 0.28	0.89	537.3 ± 24.4	0.21 ± 0.03	1.88 ± 0.38	0.84
	M	388.4 ± 5.4	0.21 ± 0.02	-0.84 ± 0.35	0.91	782.9 ± 38.0	0.17 ± 0.03	3.75 ± 0.46	0.86
Pangnirtung	F	397.9 ± 12.7	0.30 ± 0.08	0.06 ± 0.79	0.96	791.1 ± 99.6	0.21 ± 0.12	1.22 ± 1.26	0.88
	M	450.0 ± 15.3	0.28 ± 0.06	0.47 ± 0.61	0.87	1455.1 ± 127.2	0.23 ± 0.05	4.23 ± 0.38	0.90
Grise Fiord	F	432.4 ± 24.0	0.17 ± 0.05	-2.30 ± 1.29	0.91	did not converge (N = 12)			
	M	545.0 ± 117.7	0.15 ± 0.08	-0.31 ± 1.11	0.72	3897.1 ± 4180.9	0.09 ± 0.07	11.96 ± 12.06	0.79

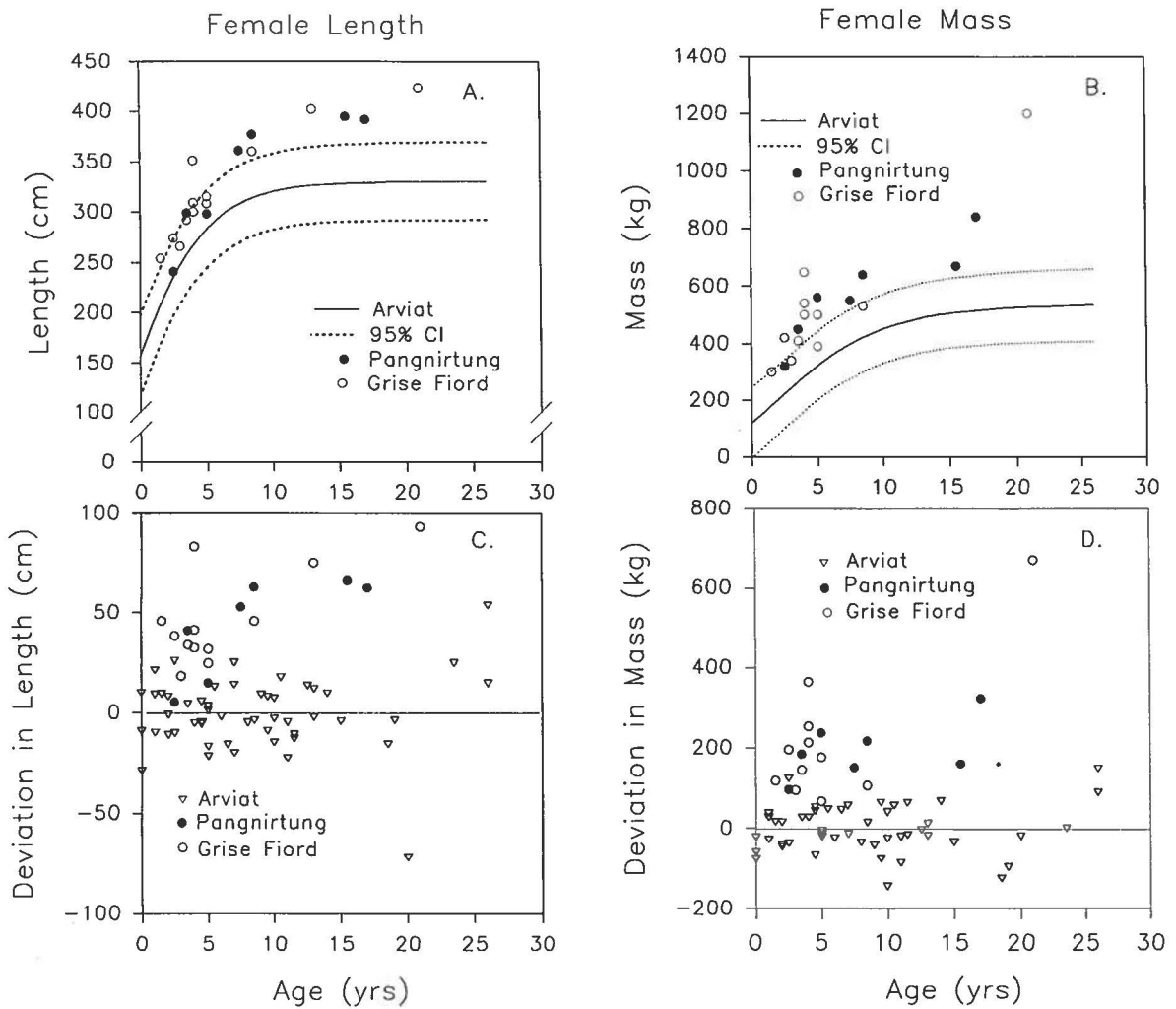


Fig. 2. Gompertz growth curves for length (A) and mass (B) of female white whales (*Delphinapterus leucas*) sampled at Arviat and deviations of length (C) and mass (D) data from that curve for whales sampled at Arviat, Pangnirtung and Grise Fiord. Gompertz growth curve is plotted with the 95% confidence interval of the population.

$$\log \text{ mass} = a + b_l \cdot \log \text{ length} + b_{ag} \cdot \log \text{ axilla girth} + b_{ng} \cdot \log \text{ navel girth} + \epsilon$$

where mass is total mass (kg), length is standard length (cm), a is the intercept, b_l , b_{ag} and b_{ng} are the coefficients associated with length, axillary and navel girth, respectively, and ϵ is the residual error.

Results

One hundred twenty-eight, 34 and 30 white whales were examined at Arviat, Pangnirtung and Grise Fiord, respectively. Due to missing data, sample sizes in various analy-

ses are sometimes less than the number of whales sampled.

The sample from Arviat was the only one to include young of the year (Table 1). The largest female and the largest male were both sampled at Grise Fiord. The oldest whales were from Arviat.

The Gompertz model converged for all data sets (sex by locations) except for mass of females sampled at Grise Fiord (Table 2). Also, for male white whales from Grise Fiord, the Gompertz model estimated an asymptote which was associated with a large standard deviation ($CV = 23\%$) and the asymptote was 13% greater than the maximum length observed.

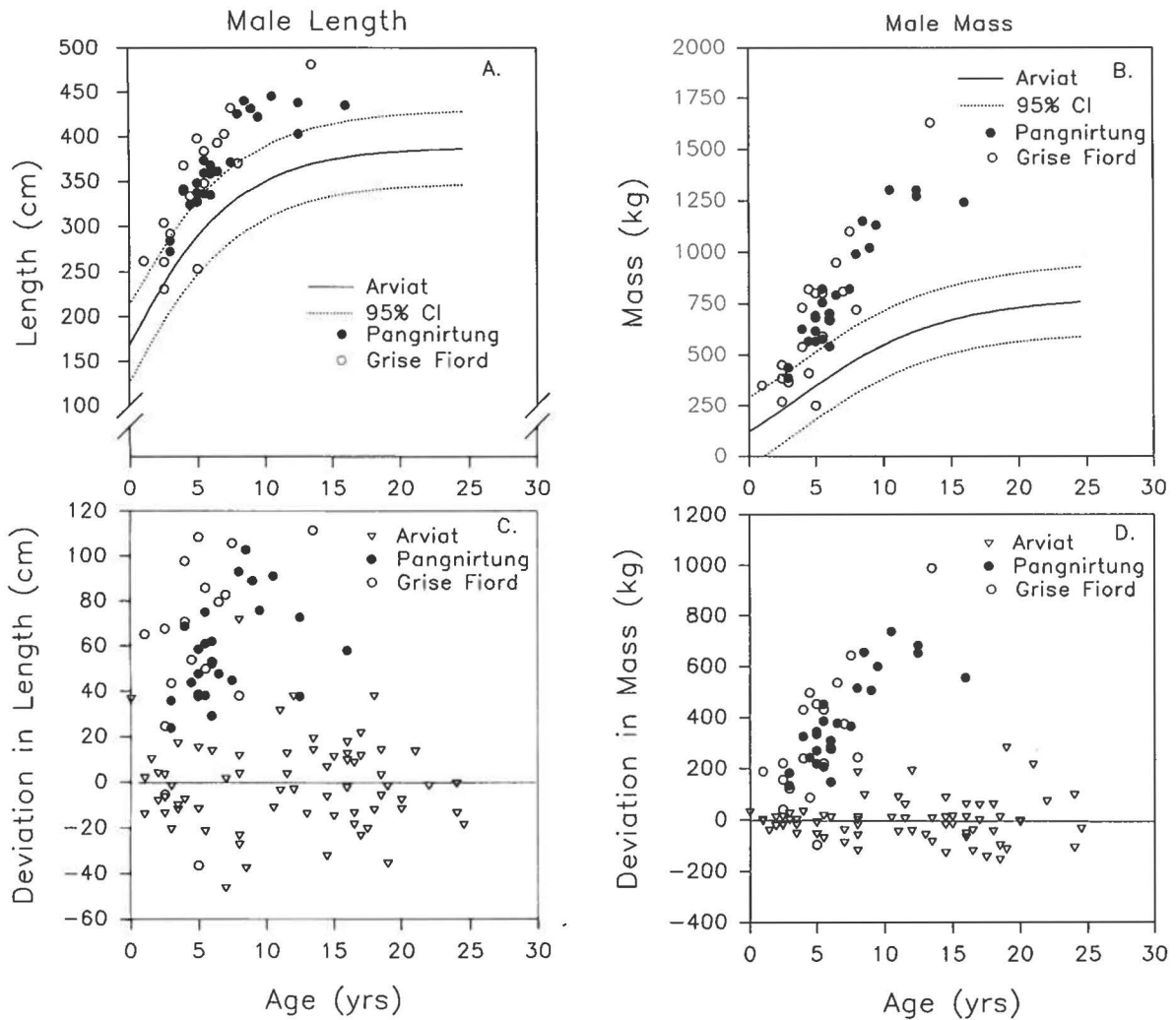


Fig. 3. Gompertz growth curves for length (A) and mass (B) of male white whales (*Delphinapterus leucas*) sampled at Arviat and deviations of length (C) and mass (D) data from that curve for whales sampled at Arviat, Pangnirtung and Grise Fiord. Gompertz growth curve is plotted with the 95% confidence interval of the population.

Sexual dimorphism

At all locations, maximum observed size was larger for males than for females. Asymptotic lengths of males were significantly greater than those of females at Arviat ($P < 0.01$) and Pangnirtung ($P < 0.05$). No significant differences in asymptotic length of males and females were detected at Grise Fiord ($P > 0.05$) where the oldest male sampled was only 13.5 years old.

Asymptotic mass (Table 2) of females and males at both Arviat and Pangnirtung were significantly different ($P < 0.01$). Males grew to a greater mass than did females. Growth-curve models did not produce testable asymptotes for females or males at Grise Fiord.

Stock differences

The asymptotic length from the Gompertz growth equation was significantly greater for whales from Pangnirtung ($P < 0.01$) and Grise Fiord ($P < 0.01$) than at Arviat for both females and males. Asymptotic mass was significantly greater at Pangnirtung for both males and females than at Arviat ($P < 0.01$). Asymptotes for Grise Fiord whales were not compared due to the poor fit (Table 2). Observed lengths and masses of both males and females from Pangnirtung and Grise Fiord were outside the 95% confidence interval of the Arviat population after age ~5–7 years (Figs 2 and 3).

For both length and mass there were significant differences between sites in the distribution of deviations about

Table 3. White whale body mass (kg) as a function of length (cm) in the form $\log \text{mass} = a + b \cdot \log \text{length}$ where a is the intercept and b is the slope. Parameter estimates are ± 1 SE. All lines were significant at $P < 0.01$. ns indicates individual parameter estimates which were not significantly different from 0 (t-test, $P > 0.05$).

Location	Sex	a	b	R ²	F _{df}
Arviat	F	-3.05 ± 0.22	2.27 ± 0.09	0.92	614 _{1,52}
	M	-2.98 ± 0.19	2.25 ± 0.07	0.93	936 _{1,66}
Pangnirtung	F	-1.13 $\pm 0.74_{ns}$	1.53 ± 0.29	0.84	27 _{1,5}
	M	-3.38 ± 0.39	2.44 ± 0.15	0.91	257 _{1,24}
Grise Fiord	F	-3.13 ± 0.77	2.33 ± 0.31	0.87	58 _{1,9}
	M	-3.10 ± 0.53	2.33 ± 0.21	0.88	125 _{1,17}

the Arviat growth curve (Figs 2 and 3) (females: $\chi^2 = 33.78$, $DF = 2$, $P < 0.001$, males: $\chi^2 = 66.04$, $DF = 2$, $P < 0.001$). The Dunn's test of all pairwise comparisons indicated that the deviations were significantly greater at Pangnirtung and Grise Fiord than at Arviat ($P < 0.05$) but that they were not different between Pangnirtung and Grise Fiord ($P > 0.05$). All deviations at the latter two sites were greater than zero and increased with age (Figs 2 and 3).

Mass-length relationships

Length explained at least 85% of the variation in mass in the six sex-location analyses (Table 3). Improvements on these fits could be obtained by the addition of girth measurements, but the most useful girth varied among

sex-location combinations and did not significantly improve the fit for males from Pangnirtung or for either females or males from Grise Fiord.

Overall, there were significant location effects ($F_{2,180} = 28$, $P < 0.01$) but not sex effects ($F_{1,180} = 1.7$, $P = 0.20$). Analysis of variance for sex differences at each location suggested that there was a difference between females and males at Pangnirtung ($F_{1,30} = 4.77$, $P = 0.04$), but this was not supported by t-tests ($P > 0.05$). Similarly, significant differences among locations indicated by ANOVA ($P < 0.01$) were not confirmed by t-tests ($P > 0.05$). A single expression relating mass (kg) to length (cm) for all the data was:

$$\begin{aligned} \log_{10} \text{mass} &= -3.29 + 2.38 \cdot \log_{10} \text{length}, R^2 = 0.92, \\ &F_{1,183} = 2027 \\ &\text{or} \\ \text{mass} &= 0.0005 \cdot \text{length}^{2.38}. \end{aligned}$$

This equation tends to underestimate the mass of long white whales sampled at Grise Fiord in the fall.

Discussion

The statistical comparison of non-linear growth curves such as those derived from the Gompertz model is not simple (e.g. Cerrato 1990), partly because of correlations among the estimated parameters. In this study, comparisons were limited to tests of differences in asymptotes and of deviations from the growth curves for Arviat to avoid problems of parameter correlation. The latter test also reduces the impact of different age distributions for the three collection sites by allowing age-specific comparison.

Comparison of mass measurements is confounded by seasonal effects due to changes in feeding and reproductive status (Brodie 1989, Stewart & Stewart 1989). For

Table 4. Asymptotic (± 1 SE) body lengths (cm) of white whales from five sites: Churchill (CH), northern Quebec (NQ), and Northwest Alaska (AK) (Doidge 1990a) and Arviat (AV) and Pangnirtung (PG) (present study). Grise Fiord data were excluded due to the high variation associated with the asymptotes. Sites which were not significantly different from each other ($P > 0.01$) are underlined. Significant differences between sexes is indicated by: ns ($P > 0.05$), * ($P < 0.05$) or ** ($P < 0.01$).

Location	CH	AV	NQ	AK	PG	Location Differences
Females						
Asymptotic length (cm)	328	331	330	359	398	<u>CH NQ AV</u> AK PG
SE	± 6	± 5	± 6	± 4	± 13	
N	77	51	55	51	7	
Males						
Asymptotic length (cm)	377	389	349	427	450	<u>NQ CH AV AK</u> PG
SE	± 14	± 5	± 10	± 8	± 15	
N	65	68	44	56	25	
Sex Differences	**	**	ns	**	*	

example, the mass-length relationships reported here, which are similar to those previously reported (Doidge 1990a), tended to underestimate the mass of longer males in the fall. Further discussion is limited to comparisons of standard length.

Sexual dimorphism

Although male white whales are widely known to be larger than females (Stewart & Stewart 1989), the degree of dimorphism reported varies among studies and stocks. Sergeant & Brodie (1969a: Fig 8) reported mean lengths for females and males of approximately 305 and 360 cm, respectively (males were 18% longer), in western Hudson Bay, 350 and 405 cm (males 16% longer) in Cumberland Sound, and 365 and 450 cm (males 23% longer) in Jones Sound. Average lengths of adult female and male white whales sampled in Cumberland Sound by Brodie (1971) were 362 and 427 cm, respectively; males were 18% longer. Mean lengths of adult, white-coloured whales from northwestern Alaska were 350.7 cm (females) and 402.9 cm (males 15% longer than females) (Burns & Seaman 1985).

Doidge (1990a) reanalysed the earlier data from western Hudson Bay (Sergeant & Brodie 1969a, Sergeant 1973) and northwestern Alaska (Burns & Seaman 1985) with his own data from northern Quebec. He did so in sufficient detail that statistical comparisons can be made with the current data (Table 4). There were significant sex differences in all but the northern Quebec sample (Table 4). Differences ranged from 6% in the northern Quebec to 18% and 19% in the Arviat and Alaska samples, respectively. Thus my analysis agrees with Doidge's conclusion that there was sexual dimorphism in size at some locations, but not that it was slight.

The degree of sexual dimorphism in size was substantial for all samples except the one from northern Quebec (Doidge 1990a). Male white whales from northern Quebec were also significantly shorter than males in a sample taken at Arviat in the same years (Table 4) (Doidge 1990a). If the male population segregates by size (Sergeant 1973, Burns & Seaman 1985) in northern Quebec, the sample may be biased toward smaller males. However it is not known if such segregation occurs at the Nastapoka River where the northern Quebec whales were caught (Doidge 1990b). Females at Arviat and in northern Quebec, collected in the same period, were virtually identical in asymptotic length (328 and 331 cm). The Arviat sample was a mix of shot and netted whales, although there may still be unknown sampling bias.

The mating system of white whales is poorly understood, and selection factors favouring dimorphism in size cannot be assessed. Such an analysis would have to consider the interaction of stock and sex differences. Moreover, relative stock size may influence the degree of apparent dimorphism if previous hunting pressure has

selectively removed larger males from, for example, the northern Quebec population.

Stock differences

Several other studies examined the body size of white whales from the same locations used in this study. Sergeant & Brodie (1969a: Fig 8) concluded that white whales from different stocks could be distinguished on the basis of size-at-age. In their study, mean lengths of females were approximately 18% shorter in western Hudson Bay (305 cm) than in Cumberland Sound (350 cm), where they were less than 5% shorter than in Jones Sound (365 cm). Males showed a similar pattern: western Hudson Bay males (360 cm) were 13% shorter than Cumberland Sound males (405 cm) which were 14% shorter than Jones Sound males (450 cm). Brodie (1971) reported average lengths of 362 and 427 cm for females and males, respectively, in Cumberland Sound. Estimates from both previous studies are smaller than estimates of asymptotic length obtained in the current study for the same regions, although detailed comparisons are not possible. Superficial comparisons suggest the same pattern, however, with the difference in size-at-age between Hudson Bay whales and Cumberland Sound whales greater than between Cumberland Sound and Jones Sound whales.

Doidge (1990a) reanalysed the original data from Sergeant & Brodie (1969a) and Burns & Seaman (1985). His asymptotes for western Hudson Bay whales are not significantly different than the present estimates for Arviat (Table 4, $P > 0.05$). Thus, although there appear to be differences between the data of the present study and those collected previously in the same areas (Sergeant & Brodie 1969a, Brodie 1971), the only data set which can be compared statistically (western Hudson Bay, Doidge 1990a) was not significantly different.

Deviations from the Arviat curve support the conclusion drawn from the comparison of asymptotes. All the deviations from Pangnirtung and Grise Fiord were positive, suggesting that size differences may occur at early ages. However, it was not until they had matured at about 7 years of age (Stewart & Stewart 1989, Høier & Heide-Jørgensen 1994, Stewart 1994) that individual white whales from these locations exceeded the 95% CI for the Arviat population. Larger asymptotic size apparently results from faster growth rates as indicated by the steady increase in the deviations from the Arviat curve (Figs 2 and 3).

White whales from Hudson Bay appear to belong to a different stock (or stocks) than those in Cumberland Sound. The similar adult body length of females from the three locations in Hudson Bay (Arviat, Churchill and Nastapoka River) does not mean that they are from a common stock. It is highly unlikely, however, that the whales sampled at Churchill belong to a different stock

than those sampled at Arviat, 250 km north along the presumed migration route (Sergeant 1973, Sergeant & Brodie 1969b).

The present analysis supports Doidge's (1990a) conclusion that Alaskan whales are longer than Hudson Bay whales, but not his assessment that this difference is small and limited in its application for stock identification. The comparison of asymptotic length indicates significant differences. Tests of deviations from the Arviat curve show significant differences. Also, for mature whales, individuals from Pangnirtung and Grise Fiord generally fall outside the 95% CI for the population at Arviat. They would be properly classified, therefore, as not belonging to the western Hudson Bay stock 95% of the time.

Such certainty does not exist for all comparisons of course. Recent studies in western Greenland (Heide-Jørgensen & Teilmann 1994) indicate a smaller asymptotic length for both males and females than I found at Grise Fiord. For males, the asymptotic length at Grise Fiord is suspect and larger males there were within the 95% CI of the estimate for western Greenland. For females, the confidence interval for asymptotic lengths of whales from western Greenland does not include the asymptotic length or maximum size of Grise Fiord females. Therefore the evidence of a shared stock between the Canadian high Arctic and western Greenland remains equivocal using size-at-age analysis.

The differences revealed by size-at-age comparisons are in good agreement with recent genetic studies. On the basis of size-at-age, white whales in western Hudson Bay are different from those in Cumberland Sound, Jones Sound and eastern Baffin Bay (off western Greenland), but they are not different from whales in eastern Hudson Bay. Cumberland Sound and Jones Sound whales could not be distinguished from each other and the separation of Jones Sound and western Greenland whales was uncertain. A study using restriction fragment length polymorphisms of mitochondrial DNA (mtDNA) indicated that eastern and western Hudson Bay whales belong to different stocks from whales in Cumberland Sound and Jones Sound (Helbig *et al.* 1989). This finding has been supported by more recent studies using mtDNA sequencing (Brown & Clayton 1993). Moreover, both genetic studies revealed stock differences where none was found in size-at-age analysis. Genetic analysis directly addresses the question of stock relationships and has greater potential to identify stocks. With developing techniques for nuclear DNA analysis, genetic studies also have the potential to provide information on stock status (*e.g.* Patenaude *et al.* 1992).

Body-size differences associated with some stocks of white whales are still of biological interest despite their waning importance to stock-identity questions. The hypothesis relating marine productivity to white whale body size (Sergeant & Brodie 1969a) has not been tested and few alternatives have been proposed. Within a species, larger body size may offer an advantage in environments

with shorter productivity pulses, hence longer periods of poor food availability (Geist 1987, but see also Dunbrack & Ramsay 1993), regardless of total productivity. Whatever the forces at work, they appear to operate differently for males and females. The relationship between variation in differing body size and life-history traits of white whales remains unknown.

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