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Short- and Long-term Fluctuations in the Size and Condition of Harp Seal (*Phoca groenlandica*) in the Northwest Atlantic

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Abstract

A total of 8 164 harp seals (*Phoca groenlandica*) were sampled off Labrador and northeast Newfoundland between November and May of most years between 1979 and 1994, a period during which the seal population increased in size. Data from an additional 640 seals were acquired from other authors (1976–79, 1988–92). By April, males grew to an average of 169.9 cm and 103.3 kg, about 4.7 cm and 4.7 kg more than females. Mass, sculp mass, core mass, girth, blubber thickness and even body length fluctuated significantly between November and May, with maximum and minimum values encountered in February and May, respectively. All seals older than 1 year displayed similar fluctuations. Juvenile males and females (<5 year) behaved similarly, but in seals of age ≥5 years, the females came back from Arctic waters in better condition than males. The drop in mass seen during the whelping period coincided with a drop in core mass, whereas sculp mass changed little or not at all. Using data for April to remove seasonal variability, young females (<5 years) were found to grow more slowly in both length and mass in the period 1990–94 than in previous observations in the same period in 1976–79, 1980–84 and 1985–89. Young males did not differ in growth rate between periods, but had lower length and mass at a given age in 1990–94 than seals from previous periods. Older seals of both sexes were in worse condition in April 1992 than in April 1982, 1983 and 1984, but did not differ from those sampled in 1981 or 1979.

Key words: Biological characterstics, body condition, body size, growth, harp seals, population size, seasonal fluctuations

Introduction

Northwest Atlantic harp seals (*Phoca groenlandica*) spend their summers in Arctic waters, feeding heavily and accumulating energy reserves mostly as blubber. In the autumn they migrate southward to winter off the coast of southern Labrador and eastern Newfoundland, or in the Gulf of St. Lawrence (Sergeant, 1991). They form large whelping concentrations in late-February/early-March near the Iles de la Madeleine or off southern Labrador, during which time they reduce their feeding. Following breeding they disperse briefly, and the females at least appear to feed and replenish their energy stores (Sergeant, 1991). From mid-April to mid-May they congregate into large moulting concentrations, during which time again they exhibit a period of reduced feeding. Soon after moulting, harp seals migrate northward. The timing of the migrations appears to be variable but generally harp seals enter the study area in October or November and leave in May or June (Stenson, unpublished data).

Although growth and morphometric measurements of harp seals have been published before (Beck *et al.*, 1993; Hammill *et al.*, 1995; Innes *et al.*, 1981; Sergeant, 1973, 1991; Stewart and Lavigne, 1980), most of the material was sampled in the Gulf of St Lawrence, with very little information from animals caught off Newfoundland. Furthermore, small sample sizes and the temporal distribution of the samples have resulted in a sketchy knowledge of seasonal changes in their mass and fat reserves, whereas core mass and length of adult seals have been assumed not to change seasonally. More detailed information on growth and seasonal cycles in morphometric variables is necessary to evaluate seal energy requirements, their potential effect on prey

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population, and alternatively, the effect of changes in the latter on the condition and number of harp seals.

In this study, we combine a very large dataset collected off Newfoundland and Labrador during the period 1979–94 to data from other researchers, to better define growth in length and in mass of the harp seal, and examine monthly changes in mass, sculp mass, core mass, axillary girth, blubber thickness and body length.

A reduction in resource availability, whether or not it is due to changes in seal numbers, environmental changes, or to human activities, can impact on seals in many ways, such as an increase in the age at sexual maturity (Laws, 1956; Sergeant, 1991), a reduction in the health, growth rate, or size of individuals (Hammill *et al.*, 1995; Innes *et al.*, 1981), or an increase in mortality. Two previous studies have attempted to detect an improvement in the size-at-age when seal numbers were declining (Innes *et al.*, 1981), and a reduction in size-at-age and in condition when seal numbers were increasing (Hammill *et al.*, 1995). In both cases, the results partially supported their hypotheses, but problems with the data prevented firm conclusions. With this larger dataset, we explore the possibility that the growth rate and the condition of harp seals have deteriorated in recent years, which have seen an increase in the size of this seal population (Shelton *et al.*, 1996; Stenson *et al.*, 1996), as well as climatic changes and the collapse of several stocks of commercial fish in the study area.

Materials and Methods

Data collection

Morphometric measurements were obtained from 8 164 harp seals between 1979 and 1994, off the coast of Labrador or the north-east coast of Newfoundland, mostly in NAFO Div. 2J+3KL (the Newfoundland dataset, NF). Seals were collected by the Canadian Department of Fisheries and Oceans researchers or commercial sealers, or as incidental catch in fishing gear. The great majority of seals were collected between the months of November and May (Tables 1 and 2). Most seals were measured within a few hours of being killed, but samples from the Labrador coast were usually frozen, and thawed before measurements were taken.

Date, time, location, sex, pelage type, and pelage condition (hair fast or loose) were noted. Standard body length (L to the nearest 0.5 cm), total mass (M_t to the nearest kg for large animals, and to the nearest 0.5 kg for smaller seals and sculp), axillary girth (G to the nearest 0.5 cm), anterior length of front and hind flipper (FF and HF to the nearest 0.5 cm) and blubber thickness (B to the nearest mm) were measured following the recommendations of the American Society of Mammalogists (1967), except that B excluded the skin. Sculp mass (M_s to the nearest 0.5 kg), i.e. the skin with blubber attached, except for the skin of hind flippers and of the tip of the front flippers, which remained with the carcass, and core girth (G_c to the nearest 0.5 cm), i.e. girth measured at

TABLE 1. Number of female harp seals collected each month during the period 1979–94[1].

	Month											
Year	1	2	3	4	5	6	7	8	10	11	12	Total
1979		3	4	220								227
1980	1	29	13	31	64						1	139
1981	35	43	78	110	97						10	373
1982	5	9	134	207	12							367
1983			55	483	66							604
1984			46	250								296
1985			2		20						2	24
1986	8	1	44		22						66	141
1987	9	23		92	36	47				1	70	278
1988				47	29	7			2	43	48	176
1989	2		13		8				1	15	27	66
1990	14		68			17	1			23	30	153
1991		7	4	8	1	6			4	29	47	106
1992	10	10		291	11	10	8			70	49	459
1993	5	16		1	42	12	22		5	72	8	183
1994	14	15	73		6					1		109
Total	103	156	534	1 740	414	99	31		12	254	358	3 701

[1] These sample sizes include seals of known age only. Another 16 males were sampled but were excluded from most analyses. 584 seals of known age were missing standard length, total mass and axillary girth.

TABLE 2. Number of male harp seals collected each month during the period 1979–94[1].

	Month											
Year	1	2	3	4	5	6	7	8	10	11	12	Total
1979		2	7	170								179
1980	7	56	7	39	67						3	179
1981	31	64	42	175	114						14	440
1982	3	20	91	434	18							566
1983			29	500	78							607
1984			16	306	4							326
1985					40						3	43
1986	5	13	13		23						79	133
1987	21	55		117	31	39	1			3	135	402
1988				40	23	8			1	15	50	137
1989			7		10	1			6	7	35	66
1990	9		22			15		1		13	60	120
1991		39	4	5		7			1	18	46	120
1992	14	44		603	13	13	8			90	23	808
1993	4	22			41	26	21		2	71	6	193
1994	31	25	23		8							87
Total	125	340	261	2389	470	109	30	1	10	217	454	4 406

[1] These sample sizes include seals of known age only. Another 41 males were sampled but were excluded from most analyses. 699 subjects of known age were missing standard length, total mass and axillary girth.

approximately the same site as G, but after removal of the sculp, were also measured. The seals were skinned using the same method as sealers, so a small amount of fat usually remained on the carcass, whereas some flesh was cut off with the sculp. Since the same three observers took the great majority of the measurements for the entire sampling period, this source of error remained relatively constant. M_t was corrected for the mass of the stomach content, but was not corrected for blood loss in shot animals, nor for the mass of the foetus in pregnant females. For measurements obtained on board ships, the accuracy of M_t and M_s was somewhat reduced by the movements of the ship in rough weather. Age was determined by counting dentinal annuli from a cross-section of a lower canine tooth (Bowen *et al.*, 1983) and assuming seals were born on March 5. Age of very young animals was determined using their coat colour and condition and the data of Stewart and Lavigne (1984).

In addition to the above dataset, D. M. Lavigne (Department of Zoology, University of Guelph, Ontario) provided the measurements for the 204 seals used in the Innes *et al.* study (1981), and M. O. Hammill (Department of Fisheries and Oceans, Institut Maurice-Lamontagne, Quebec) provided the measurements for another 436 seals from the Hammill *et al.* study (1995). The Lavigne data included mostly seals from the Gulf of St Lawrence (Div. 4RS), but also 52 seals from the Front, 36 from the Northwest Territories and 5 from West Greenland, whereas the Hammill data included 425 seals from the Gulf of St Lawrence (Div. 4RS) and 11 from Hudson Strait.

The following variables were computed from the measured variables:

- core mass ($M_c = M_t - M_s$)
- sculp ratio ($SR = M_s \times 100/M_t$)
- volume (an estimate of body volume based on an ellipsoidal model of seal shape, $V = \frac{L \times G^2}{6000\pi}$)
- sculp volume ($V_s = V - \frac{2\pi LG}{3000\,(2\pi - B)}$)
- estimated core girth ($\hat{G}_c = G - 2\pi(B + 0.3)$)

Data validation

To distinguish between 'valid' extreme cases and errors (measurement, transcription or key punching errors) in the NF dataset, we looked for inconsistencies in the ways the morphometric variables varied together by calculating linear regressions between selected measured and calculated variables. Cases with a studentized residual ≥3 or ≤-3 were verified against the original data sheets, and corrected when a mistake was found. Otherwise, cases with a studentized residual ≥4 or ≤-4 were marked as outliers. When studentized residuals are normally distributed, only 0.006% of them should lie outside 4 standard deviations (Runyon and Haber, 1971). Therefore, a data point with such a high studentized residual would be expected only once in a dataset of 10 000 cases.

The following tests served to detect outliers:

- regression of $\log_{10}(M_t)$ on $\log_{10}(V)$, for each sex
- regression of $\log_{10}(M_s)$ on $\log_{10}(V_s)$, for each sex
- multiple regression of $\log_{10}(G)$ on $\log_{10}(L)$, $\log_{10}(\sqrt[3]{M_t})$ and $\log_{10}(B)$, for each sex in seals older than 30 days, and for both sexes combined in younger seals
- regression of FF on HF, for each sex
- regression of $\log_{10}(G_c)$ on $\log_{10}(\hat{G}_c)$, for each sex

Thirty-one cases were rejected because one or more of the variables L, M_t or G was suspect, bringing the final sample size in the NF dataset down to 8 165. Some variables were set to missing in a few other cases as a result of these analyses: FF and HF in 12 cases, G_c in 7 cases, and M_s and B in 11 cases.

Statistical analyses

Gompertz growth curves of the form $y = y_\infty e^{(-b \cdot e\ (k \cdot age))}$, where b and k are constants (Fitzhugh, 1975; Kaufmann, 1981), were fitted to M_t and L using the NLIN procedure of SAS (SAS Institute, 1989). Two Gompertz growth curves were compared statistically by checking if the asymptotic 95% confidence interval for the estimated difference in any of the growth curve parameters included zero.

Means were compared by analysis of variance (ANOVA, 2-way ANOVA). Regression lines were fitted by the least-square method. Regression lines were compared by first testing for the parallelism of the slopes, and if necessary comparing the intercepts with analysis of covariance (Pedhazur, 1982). Post-hoc pairwise comparisons of means or of adjusted means with 1 df contrasts (Neter *et al*., 1990) were used to identify which groups differed from each other. The risk of type I error for the family of comparisons was kept at $\alpha = 0.05$ by using Sidák's multiplicative inequality (Kirk, 1982). ANOVA and regressions were analyzed with SAS version 6 (SAS Institute, 1989) or SuperANOVA version 1.11 (Abacus Concepts, 1989).

Results and Discussion

Growth curves

Body length is usually preferred to body mass to study growth in pinnipeds because of the large seasonal variations in fat reserves and thus body mass. However, length too can vary seasonally in pinnipeds (see Trites and Bigg, in press). If this is the case for harp seals, the parameters of the growth curve could be influenced by the seasonal distribution of the samples. To reduce seasonal variability, only seals sampled in April were selected in the computation of growth curves. This was the month for which we have the largest sample sizes, and was close to the minimum in condition for the harp seal (see below). Therefore, the resulting growth curves approximate "lean growth".

Figure 1 shows the growth in length and in mass of female harp seals sampled in April. Figure 2 shows the growth of males. Despite a range of about 40 cm and 60 kg for any given age, the Gompertz model provided a good fit: age explained 83 to 89% of the variation in length or mass for both sexes. For L, all three parameters of the Gompertz curves differed significantly between sexes, whereas for M_t only $M_{t\infty}$ and *k* were different. The differences in *k* and *b* (for length curves) were small, and only the large sample sizes allowed their detection. However, their biological significance was small, considering the scatter of points about the fitted curve. Asymptotic size for both L and M_t remained different between sexes even when a common *b* and *k* were used. Therefore, asymptotic values of length and mass were slightly but significantly larger in males than in females. Fisher (MS 1955) and Innes et al. (1981) found no differences in L_∞ between sexes, but sample sizes were smaller than in the present study. Furthermore, data from March through September were pooled in Innes *et al*. (1981). Sivertsen (1941) found a difference between L of female (168 cm, n = 104) and male (172 cm, n = 173) 'saddle' harp seals sampled in the White Sea in March through May. Using his data, we found that this difference was significant (Mann-Whitney, normal approximation, Z = -3.69, p = 0.0002). Hammill *et al*. (1995) also found males to grow longer than females, although they found no difference in the other parameters of the growth curve, possibly because of a smaller sample size than in our study, or because of the added variability due to pooling data from different months. Hammill *et al*. (1995) noted that the presence of very large females in the dataset of Innes *et al*. (1981) explained the lack of difference between L_∞ of both sexes in that study. The fact that Innes *et al*. (1981) obtained a higher proportion of females than males in March and in the summer months in the Arctic, when L is higher (see below), is probably another contributing factor.

L_∞ was 169.9 cm for both sexes in Innes *et al*. (1981), 165.3 and 170.4 cm for females and males respectively in Hammill *et al*. (1995), and 164.1 and 168.8 cm for females and males in the present study. Lower asymptotic length in the present study was

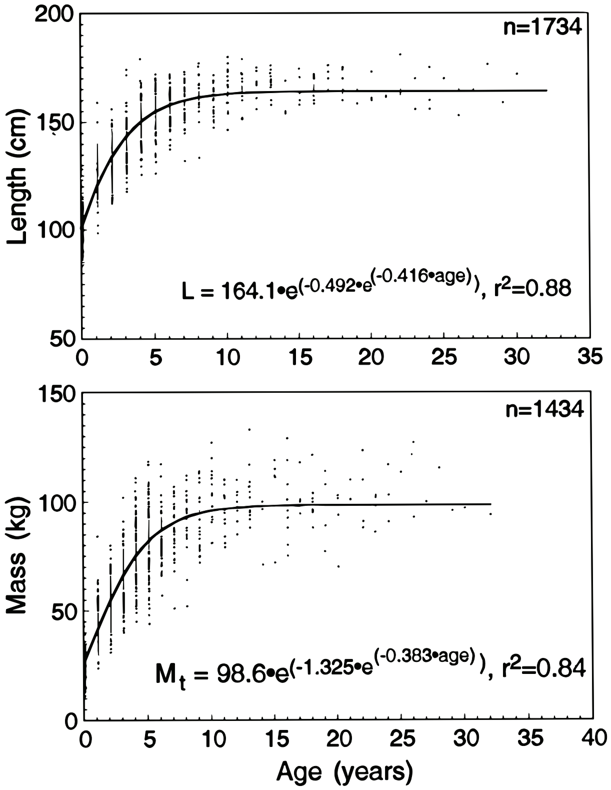

Fig. 1. Growth in standard length (L) and total mass (M_t) of female harp seals sampled in April, including the fitted Gompertz growth curves.

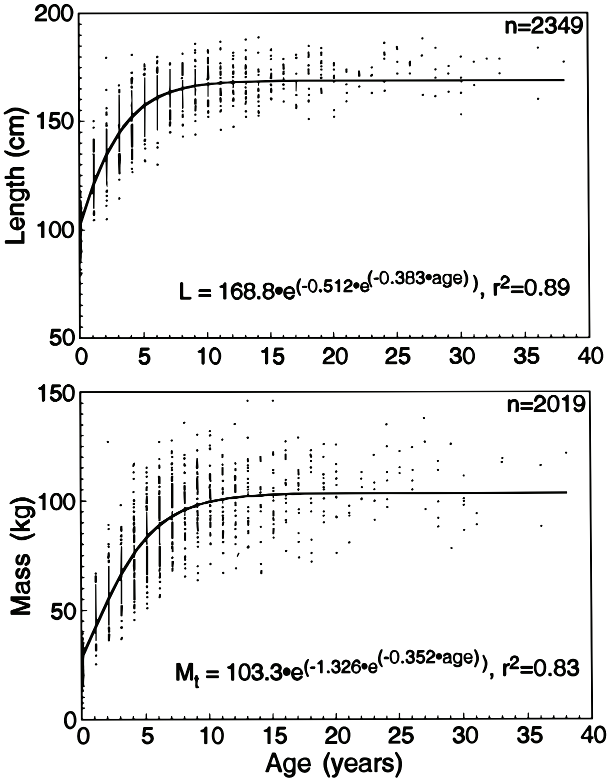

Fig. 2. Growth in standard length (L) and total mass (M_t) of male harp seals sampled in April including the fitted Gompertz growth curves.

most likely due to the fact that unlike the other studies, fat seals from February or March, or seals from Arctic waters in the summer, were excluded. The much lower asymptotic mass seen in Fig. 1 (98.6 kg) and 2 (103.3 kg) relative to that in the study of Innes *et al.* (1981, 129.9 kg) was also probably due to these differences in seasonal coverage between studies.

No newborn were included in the calculation of the Gompertz curves (because we selected only seals sampled in April), therefore we provide some descriptive statistics for newborns (n = 70). There were no difference between males and females for all variables tested, and both sexes were pooled before computing summary statistics (Table 3). Length and mass at birth were 85.99 cm and 9.26 kg, respectively.

For some of the analyses that follow, it was useful to regroup the subjects into age-classes with similar morphometric characteristics. Although growth in L and M_t was reduced after 5 years, we wanted to define one age-class where growth would be virtually nil, to facilitate some seasonal and annual comparisons. Thus adults were defined as the age-class when an average seal had completed 95% of its growth in length in April (growth = $L_\infty - L_0$, where L_∞ is the asymptotic length in April, and L_0 is length at birth from our sample of 70 newborns). The cutoff value was set at 8 years, when harp seals had completed more than 95% of their growth in length, and more than 91% of their growth in mass (in April). By that age, females and males had reached about 98% of L_∞ and 93% of $M_{t\infty}$. Pups were seals <1 year, juveniles displayed rapid growth, the cutoff value being the inflection point (fitted by eye), 5 years. Adolescents grew more slowly (5 ≤ age <8). At age 5, harp seals had completed at least 85% of their growth in length, and reached 93% of L_∞.

Seasonal fluctuations

It is well known that harp seals have a thick blubber layer during the winter months. Figure 3 shows the extent of the monthly fluctuations in M_t. Pups grew fairly steadily from birth to February, but this will not be discussed further here. The other age-classes displayed a similar pattern of mass fluctuations. Generally, mass peaked in February, then declined by about 30% through April (when growth curves were computed), and dropped by

TABLE 3. Descriptive statistics for the main morphometric variables (text provides units) of newborn harp seals. There was no difference between males and females for all variables, and both sexes were pooled.

	n	Mean	Std. Error	Minimum	Maximum
L	70	85.993	.626	74.0	100.5
t	70	9.263	.186	4.9	11.8
M_S	67	2.621	.068	1.3	4.2
M_C	67	6.736	.138	3.6	8.7
G	69	46.370	.422	38.0	55.0
G_C	26	36.481	.539	31.0	41.0
FF	70	17.029	.173	11.0	19.5
HF	70	22.393	.181	18.0	26.0
B	70	.117	.045	0	3.1

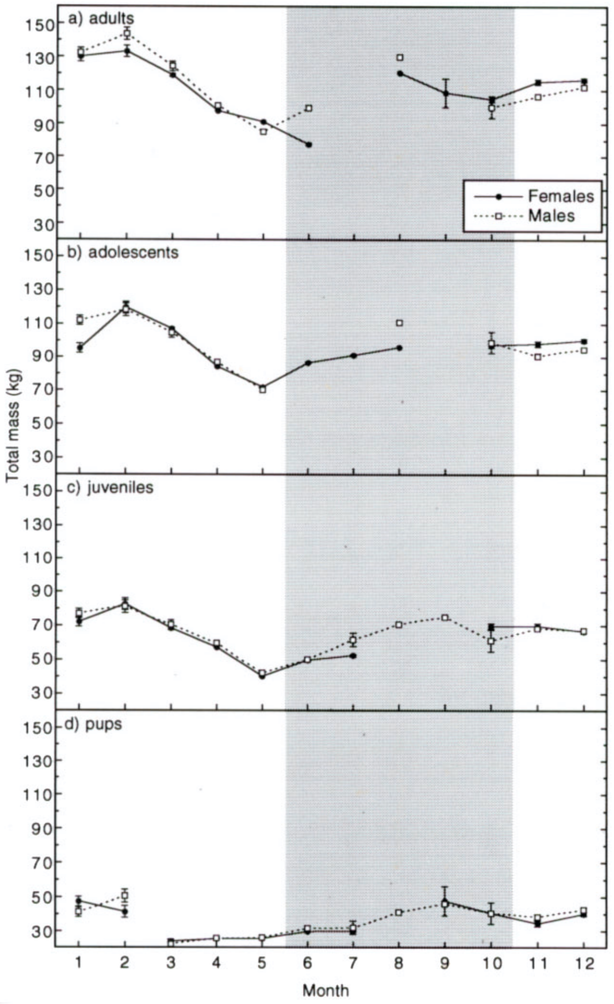

Fig. 3. Seasonal fluctuations in total body mass (M_t) for 4 age-classes of harp seals of both sexes. Means and standard errors are displayed. Pups are <1 year, juveniles are <1 year and <5 years, adolescents are ≥5 years and <8 years, and adults are ≥8 years. The shaded area represents the period when sample sizes were small. These points were excluded from statistical analyses.

another 10–15% in May, when a minimum was reached. Data were too scant between June and October (shaded area in Fig. 3) to assess whether seals continued to lose mass, and to judge the extent of fattening when the seals were in Arctic waters, but if they gained much mass (as suggested by the points for August), they lost a good proportion of it during their migration back. By November, when seals were abundant again in the study area, their M_t was about 20% off peak values. Therefore, harp seals were feeding in the study area when they gained the remainder of their M_t. Beck *et al*. (1993) also found a further increase in fat reserves of harp seals after they entered the Gulf of St. Lawrence.

A 2-way ANOVA (sex × month) was performed on each panel of Fig. 3. In juveniles, sexes did not differ in mass each month, nor in the pattern of changes between months. The interaction was significant in adolescents and adults, however, this appeared to be in part because females entered the study area heavier than males, although they were of about the same mass (adolescents) or lighter than males (adults) in January–April. The decline in mass observed between February and March was significant for all three older age-classes and both sexes. The time scale used, however, did not allow us to confirm the increase in M_t of females between parturition and moulting seen by Sivertsen (1941) and Sergeant (1973; 1991).

Figure 4 shows similar fluctuations in sculp mass. Again, juveniles of both sexes could not be discriminated, whereas the sex, month and the interaction term, were all significant in adolescent and adults. The heavier M_s of adult and adolescent females in November and December, confirmed that the gain in M_t observed in Fig. 3 was mostly due to fat accumulation in the blubber, and not pregnancy. A significant decline in M_s between February and March was only seen in adult males,

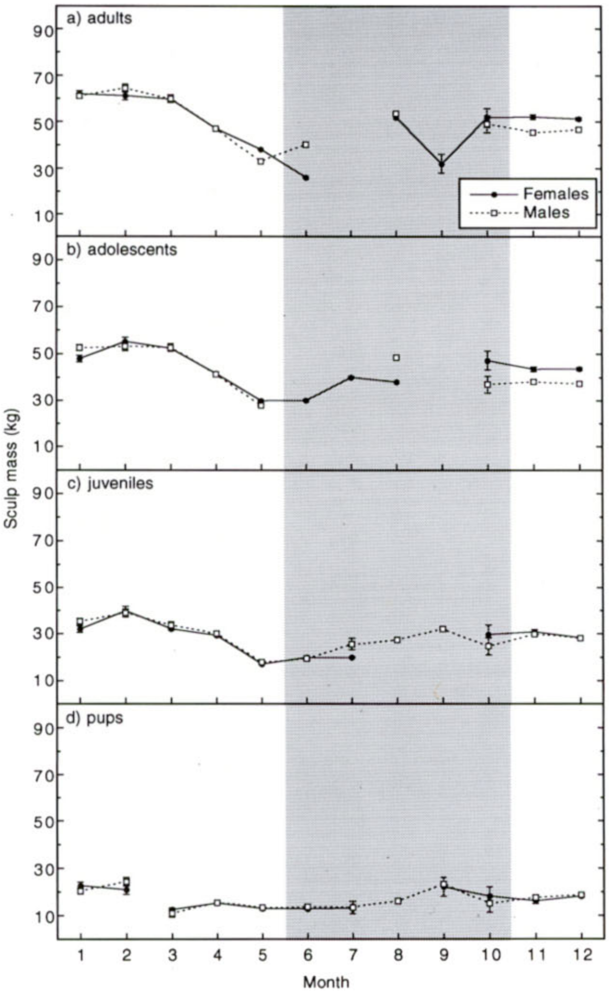

Fig. 4. Seasonal fluctuations in sculp mass (M_s) for 4 age-classes of harp seals of both sexes. Details are as in Fig. 3.

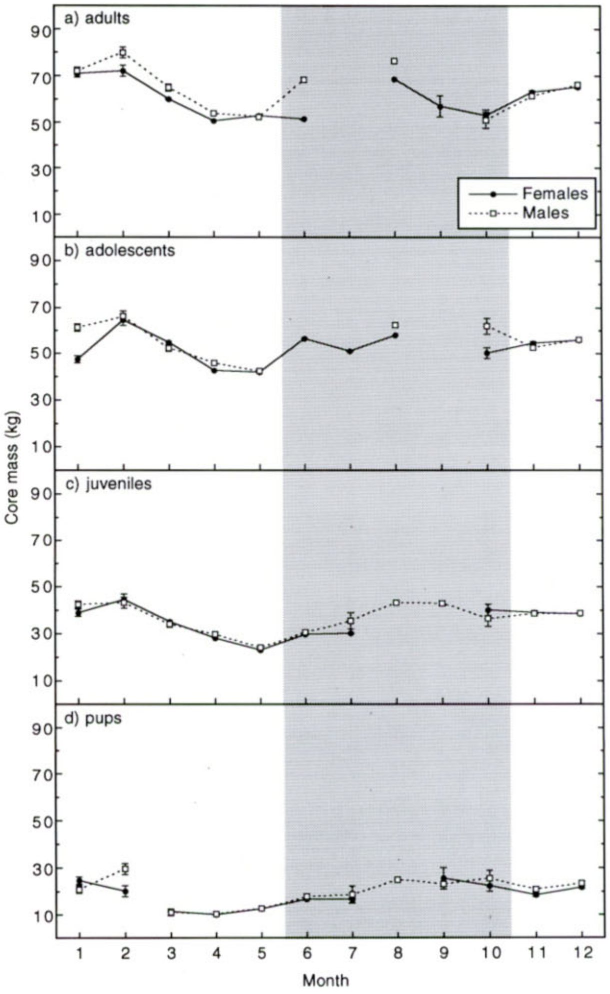

Fig. 5. Seasonal fluctuations in core mass (M_c) for 4 age-classes of harp seals of both sexes. Details are as in Fig. 3.

even though all age-classes and sexes lost M_t during this period. Even in adult males, however, the sculp loss (averaging 4.5 kg) was insufficient to fully explain the reduction of M_t (20 kg) between February and March.

This apparent discrepancy was due to a significant decline in core mass between February and March for all age-classes and sexes (Fig. 5). This is in contrast with the finding of Stewart and Lavigne (1984) that core mass did not change significantly during March in each of 4 years (1976, 1978–80), whereas sculp mass declined during each one of these years. However, their study and ours have a different time resolution, and a direct comparison of changes in sculp and core mass should be interpreted cautiously. In future work, we will reanalyse our results on a finer time scale. It is not clear at this point if lipids (about 9% of the harp seals' lipid reserves in winter are in the carcass, Beck *et al.*, 1993) or proteins are utilized, or if the amount of water in the core changes. This decline in M_c suggests that it is beneficial for the animals to maintain blubber thickness at this time of the year, presumably for thermoregulation, even in a situation of negative energy balance (see Beck *et al.*, 1993). It is a bit surprising that the decline in M_c between February and April was so similar for adults of both sexes, considering that females lost pup and placenta during this period. The decline in M_t from March to May was due to a loss of both M_s and M_c (Fig. 4 and 5), even though past studies attributed it almost exclusively to a loss of blubber (Sivertsen, 1941).

Girth should increase and decrease with M_t for any given age-class, since it does not discriminate between mass gains due to blubber or core. This was confirmed in Fig. 6, which shows seasonal changes in G that were identical to those found in M_t. Figure 7 illustrates monthly changes in blubber thickness. Fluctuations in B were in good agreement with Sergeant (1973) results. In both studies, B of males remained high until April, just as did M_s. Both studies also found B of large females to decline during March, period during which they did not experience a decline in M_s. This discrepancy could not be explained at this point. Finally, Fig. 7 shows that females have thicker blubber than males in November and December, which accounts for their heavier M_t and M_s at the time.

Body length is usually regarded as constant in fully grown phocid seals, an implicit assumption when data from different times of the year are pooled to compute a growth curve. Figure 8 shows that in harp seals, L cycles in parallel with M_t, although the oscillations in L were less pronounced than those in M_t. Such oscillations in L have been reported for northern fur seals (*Callorhinus ursinus*) (McLaren, 1993; Trites and Bigg, in press). In all 3 age-classes, L of harp seals changed similarly between months for both sexes. In adults, the oscillations in length were of about 7 cm or 4%. They increased to 11.6 cm (7%) in adolescents, and to 22 cm (15%) in juveniles. This was at odds with a comparison of Gompertz growth curves fitted to February and April data (Fig. 9). For each sex, the

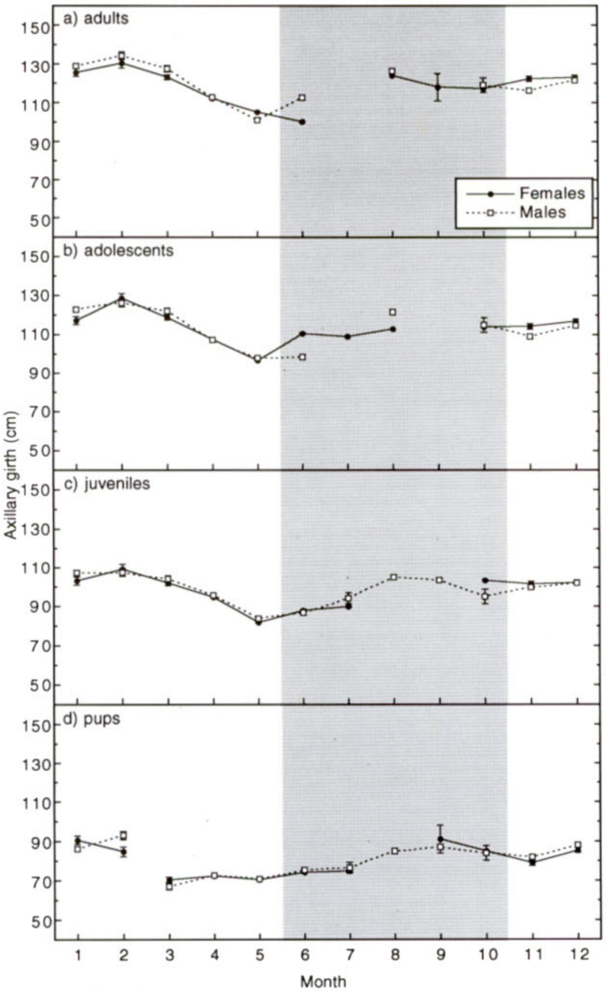

Fig. 6. Seasonal fluctuations in axillary girth (G) for 4 age-classes of harp seals of both sexes. Details are as in Fig. 3.

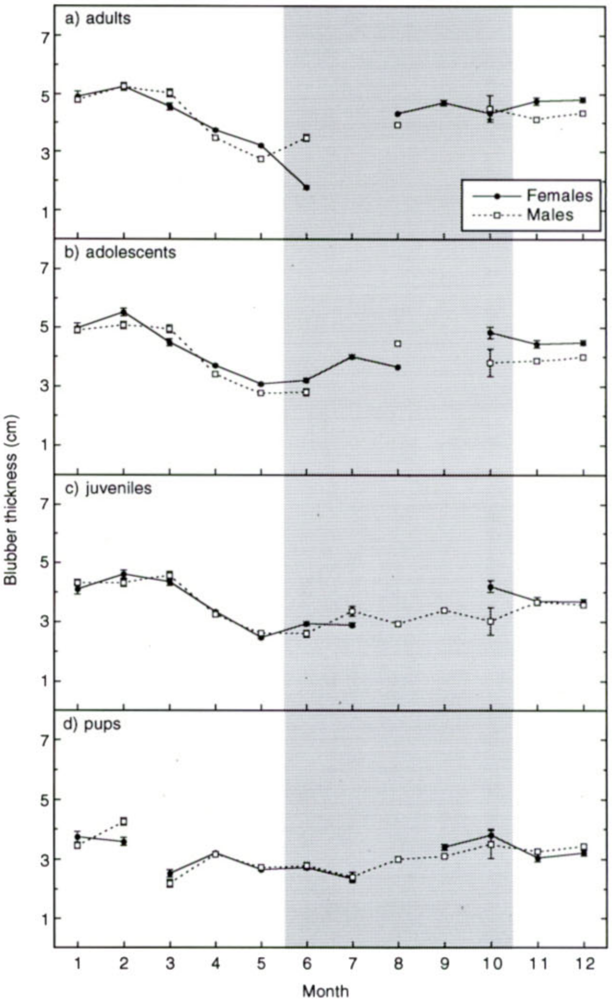

Fig. 7. Seasonal fluctuations in blubber thickness (B) for 4 age-classes of harp seals of both sexes. Details are as in Fig. 3.

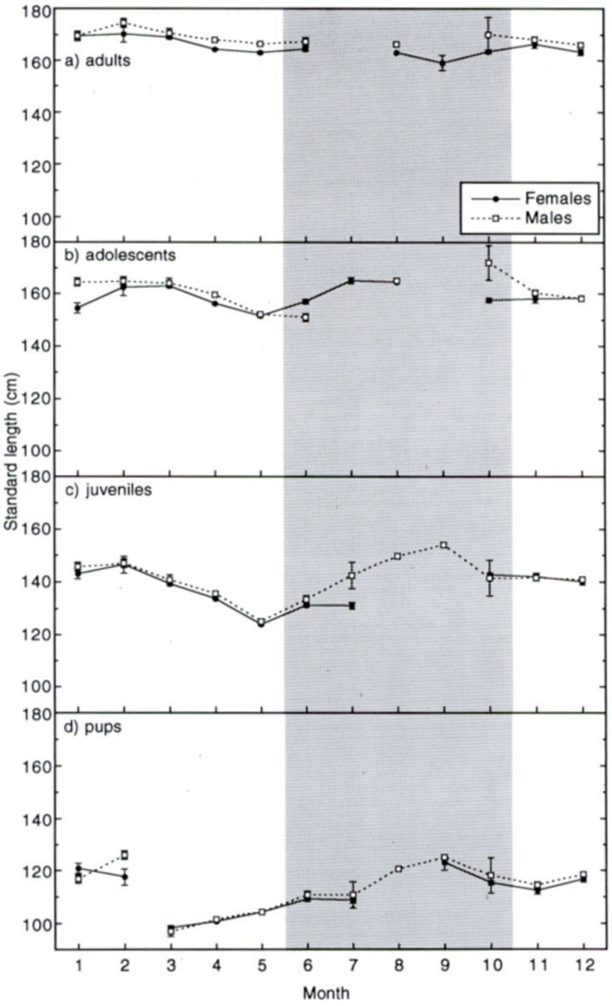

Fig. 8. Seasonal fluctuations in standard body length (L) for 4 age-classes of harp seals of both sexes. Details are as in Fig. 3.

curves for the two seasons were significantly different, for both L and M_t. However, the amplitude of the oscillations increased with age until seals were fully grown. This discrepancy was in part due to the fact that the growth curves contrast the month of February and April, not February and May. Furthermore, an artifact was introduced by pooling seals into age classes. On the growth curves, L in April was either compared to L during the preceding or the following February (seals 0.167 years younger or 0.833 years older, respectively). But in Fig. 8, age in April was 1.668, 1.411, 1.115 and 1.005 years less than in February for juvenile females, juvenile males, adolescent females and adolescent males, respectively (Table 4). Age was based on a birth date of March 5; as a result, samples taken in April contained many seals that had just entered a new age-class, and conversely, samples taken in February contained seals just about to enter a new, larger age-class.

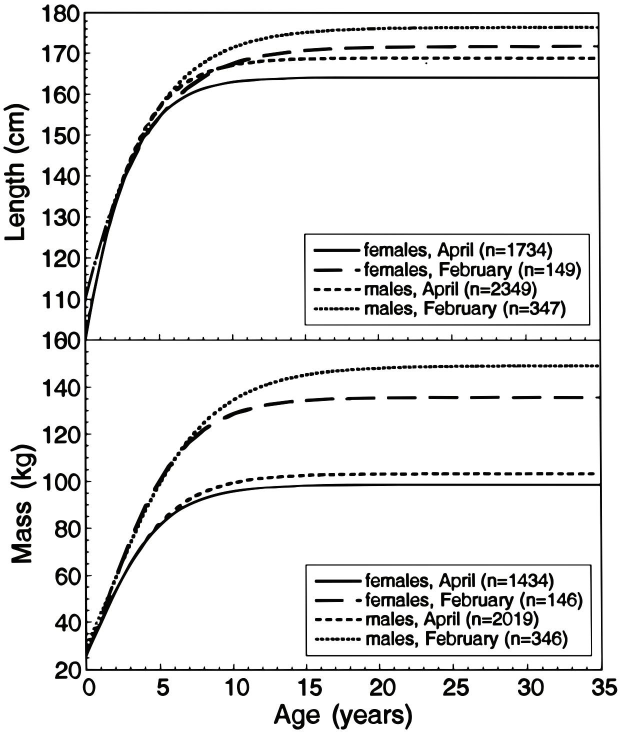

Fig. 9. Comparison of Gompertz growth curves of harp seals calculated for two seasons.

Fisher (MS 1955) thought that a thick blubber layer would result in a tightening of the skin which "pulled in" the animals so that they did not stretch out as much when laid out on the ground. Our results showed that the opposite happens: L increases with M_t. When laying seals on the ground to measure L, one often notices that quite a bit of variation in L can be obtained according to how much the head protrudes from the neck. We tried to place the head in a natural position, but it is possible that the head was less likely to be "pulled in" if the skin around the neck had a thick blubber layer. It is also possible that body mass exerted more stress upon the vertebral column in a fat seal than in a thin seal, resulting in an apparent increase in L (Trites and Bigg, in press). Bigg (1979, cited in Trites and Bigg, in press) proposed that seasonal variation in water content of the cartilage and connective tissues separating the body components, driven by changes in levels of pregnancy hormones, could explain seasonal changes in L of females. This appeared unlikely here, because both males and females, and even immature animals, showed this cycle in L. It is possible that changes in body water content due to causes other than pregnancy

TABLE 4. Mean age (years) of harp seals by sex, age class and month.

Sex	Age-class	Month	Mean	Std. Error	n
Female	Juvenile	1	3.172	.141	64
		2	3.909	.146	49
		3	2.699	.134	68
		4	2.241	.034	979
		5	1.810	.059	210
		11	3.346	.096	129
		12	3.121	.072	218
	Adolescent	1	6.634	.308	8
		2	6.958	.133	36
		3	6.028	.079	108
		4	5.843	.047	262
		5	6.006	.207	16
		11	6.369	.101	50
		12	6.491	.130	40
	Adult	1	15.588	1.414	28
		2	18.412	.769	83
		3	15.075	.281	320
		4	13.652	.402	184
		5	14.739	1.054	26
		11	15.693	.962	53
		12	14.477	.723	59
Male	Juvenile	1	3.543	.140	59
		2	3.757	.139	70
		3	2.518	.166	58
		4	2.346	.033	1101
		5	1.778	.056	237
		11	3.344	.105	104
		12	3.097	.061	293
	Adolescent	1	6.580	.164	24
		2	7.001	.113	61
		3	5.990	.126	41
		4	5.996	.038	457
		5	6.031	.273	12
		11	6.459	.116	52
	Adult	12	6.464	.100	63
		1	15.664	.920	53
		2	18.569	.492	227
		3	13.720	.477	135
		4	13.843	.275	476
		5	15.560	2.238	11
		11	12.934	.661	45
		12	13.604	.545	79

hormones were involved. The last hypothesis examined by Trites and Bigg (in press) was that because of the effect of gravity on the vertebral column, seals that were out of water for extended periods might be shorter. This hypothesis was ruled out for the harp seal, because seals spend quite a bit of time out of water in March, yet they were longer than seals in April or May. Furthermore, it was unclear whether gravity would shorten an animal whose vertebral column was held horizontally.

Figure 9 also illustrates the potential impact of pooling data from different months in comparing morphometric measurements or growth curves of harp seals: the difference in asymptotic length of curves only two months apart was greater than the difference between males and females for either month.

Many studies of pinnipeds make use of condition indices to compare the amount of fatness in different months or years:

$$\frac{G \times 100}{L}$$

or Smirnov's fatness index (Smirnov, 1924, cited in Sivertsen, 1941), used by Sivertsen (1941) and Sergeant (1973; 1991);

$\frac{(M_s - \text{skin mass}) \times 100}{M_t}$ or proportion of blubber mass to total mass, used by Sivertsen (1941);

$\sqrt{\frac{L}{M_t} \times B}$ used by Ryg *et al*. (1990) as an estimate of proportion of blubber to total mass.

Such indices are supposed to make the measure of fatness independent of L (Sivertsen, 1941), and are often used to pool data from animals that vary widely in size. Figure 10, however, shows that the indices were still correlated with body length. We calculated a condition index (CI) similar to the one used by Trites and Bigg (1992):

$$CI = \frac{M_t}{\hat{M}_t} \qquad \text{where } \hat{M}_t = aL^b \text{ (Figure 11).}$$

Seals younger than 1 year were excluded from the mass-length relationship because they were beaters in post-weaning fast, and were light compared with older seals of similar length. Because pups were excluded from the computation of the mass-length relationship, CI was not independent of size for very short seals. However, there was no correlation between CI and L for seals longer than about 110 cm.

Figure 12 shows the seasonal changes in CI for the 4 age classes. CI did not discriminate between changes in accumulation of blubber or in core mass. Therefore, Fig. 12 shows pretty much the same trends as did Figure 3. The small but significant seasonal changes in L cause CI to slightly underestimate the amplitude of seasonal changes in M_t (Table 5). This is because seals are, on average, longer in February than in April, and thus $\hat{M}_t$ is overcorrected for L.

It is important to notice that the use of such a condition index did not guarantee that all sizes and ages can be pooled in comparisons between months or between years. Even after removing the effect of L, there remained differences in CI due to age, both because age affects condition even in the month for which CI was designed to produce 1.0, and because seals of a different age may have different seasonal cycles of mass changes. For instance, the peak CI values, obtained in January and February were lower in juveniles than in older seals. This is perhaps better seen in Fig. 13. Even in April, when the mass-length relationships were computed, seals about 5 years or younger were lighter, relative to their length, than older seals. Furthermore, seals need to reach about 10 years to have the largest fluctuations in condition between winter and spring (see also Fig. 9, growth in M_t in February and April). Figure 13 also shows that males of all ages reached very low condition values in May, whereas older females remained at the levels they had reached in April, but this was probably an artifact of the small number of old females sampled in May. Males of all ages arrived in our waters in relatively poor condition, whereas females 5 years and older were in much better condition. However, males' condition improved very fast between December and January. Females ≥18 years seemed to reach maximum condition later (February) than younger females (January), but again this could be an artifact of the very small number of older females sampled in January.

Long term fluctuations

Previous attempts at relating the impact of increased population levels on the health of harp seals relied on comparisons of growth curves computed for different periods of data collection. Innes et al. (1981) found that a growth curve fitted to their sample resulted in a larger size at age 0, and a larger L_∞ than when the same curve was fitted to data collected when seals were more numerous. But no statistical comparison was done because of problems with the older dataset. Hammill *et al*. (1995) were able to compare growth curves of harp seals computed for two time periods statistically, but were not able to make definitive conclusions as to a possible deterioration in growth accompanying the increase in harp seal population. The authors noted that differences in the distribution of ages and dates of collection for both samples impaired the analyses, and the results shown in the present study emphasize the potential impact of such problems.

Comparing growth curves is not the most sensitive technique to detect possible effect of increasing seal population or declining food resources on seals, because animals from different age-classes are likely to respond differently. Studies in terrestrial mammals have shown that foetal growth, as well as neonatal growth during lactation, can be affected by the condition of the mother and/or the quality and quantity of food available to her (Geist, 1978; Thorne *et al*., 1976), and the same has been suggested for harp seals (Smirnov, 1927, cited in Sivertsen, 1941). Young, growing animals should show reduced growth when resources are limited. Since growth in length seems to stop at around 8 years, the length of older individuals probably reflects conditions encountered during gestation, lactation and the first few years of life, rather than current resource conditions (Smirnov, 1927, cited in Sivertsen, 1941; Stewart and Lavigne, 1984). For instance, even though Trites and Bigg (1992) found differences in non-parametric growth curves of northern fur seals (*Callorhinus ursinus*) for different

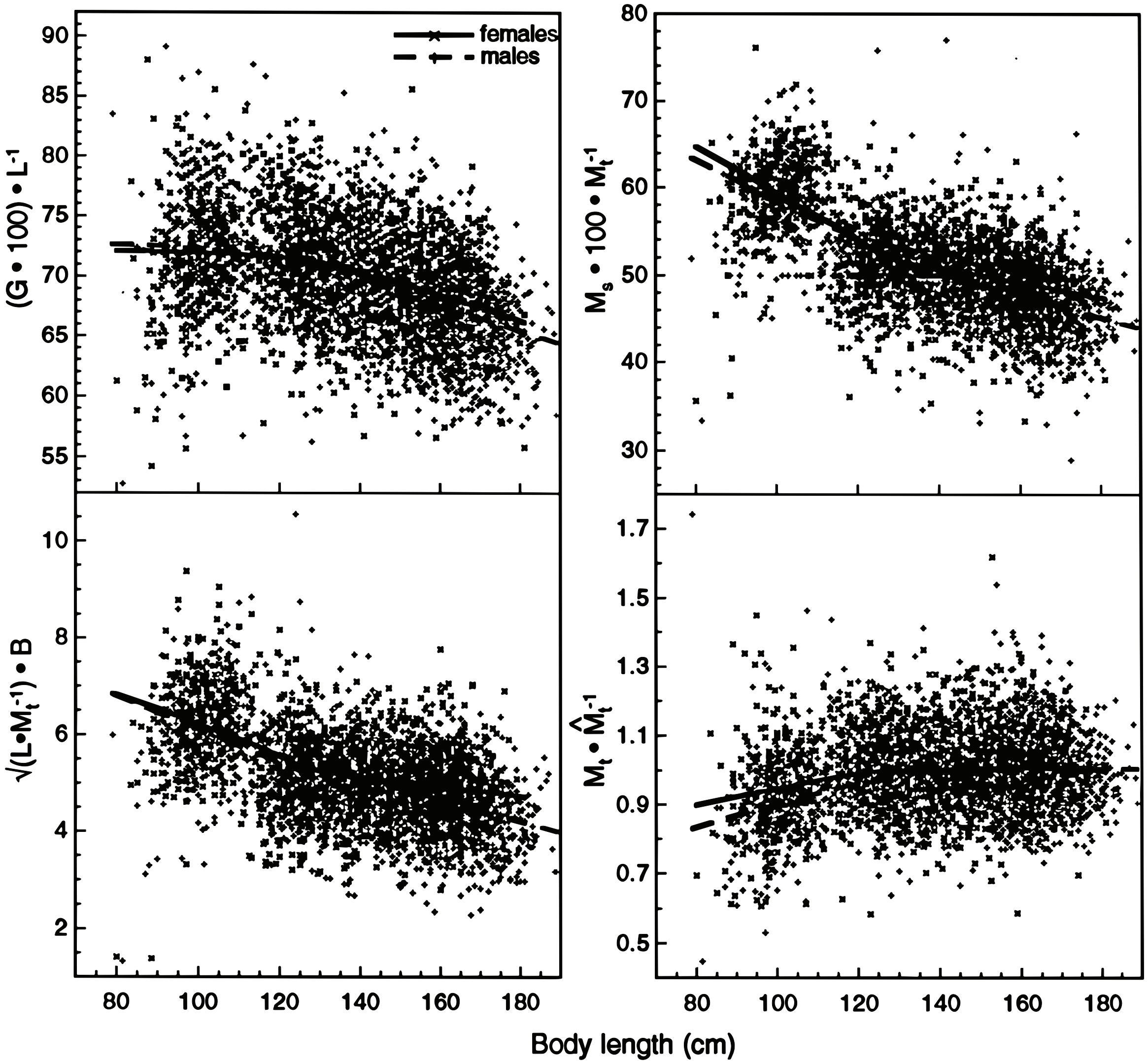

Fig. 10. Relation between various indices of condition (CI) and standard body length (L). All indices were computed using seals sampled in April. Upper left panel: Smirnov's index (1924, cited in Sivertsen, 1941); upper right panel: ratio of sculp to total mass, a close approximation of Sivertsen's proportion of blubber to total mass (1941), since M_s is highly correlated with blubber mass in harp seal (Beck *et al.*, 1993); lower left panel: Ryg *et al.* (1990) estimate of Sivertsen's proportion of blubber to total mass; lower right panel: condition index used in this study, computed as the ratio of measured total mass to mass expected from the mass-length relationship observed in April. The lines were fitted by the locally weighted (60%) least squared error method (Abelbeck Software, 1993).

time periods (e.g., 1958–62, 1963–68, and 1969–74), the curves for all 3 periods converged in older animals. Thus parameters other than asymptotic size are probably the most important ones to compare. Such comparisons are probably better done by excluding older animals: the parameters of a Gompertz curve are often correlated, and the presence of older animals whose present size does not reflect resource availability could affect all parameters.

Therefore, we decided to look for differences in growth rate as well as in size at age when comparing young animals sampled in different periods, whereas we looked for differences in condition, not size, in older animals collected in different time periods.

Birth mass and pup growth. Small sample sizes prevented us from comparing birth mass between years. Birth mass was 9.3 kg (Table 1) for the period

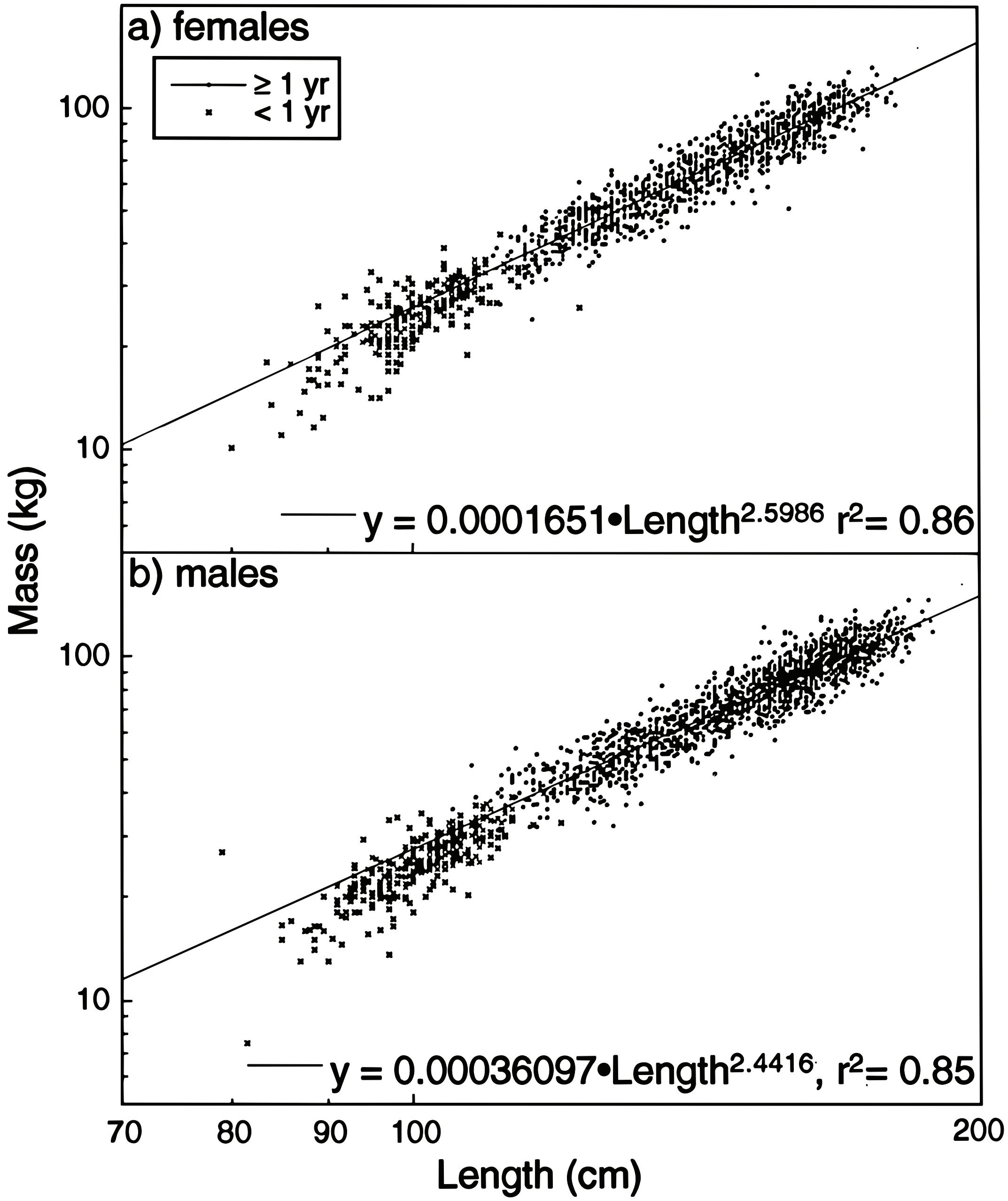

Fig. 11. Relationship between total mass M_t and standard body length (L) in female and male harp seals sampled in April.

1980–94 (with the bulk of the data from 1982, 1983 and 1990, with 21, 15 and 16 newborns, respectively). This was 1.5 kg (14%) lower than that of Stewart and Lavigne (1980, mean of 10.8, n = 40), whose data were collected between 1976 and 1979. Growth rate during lactation, however, was 2.7 kg/day (Fig. 14), a bit higher than the 2.2 to 2.5 kg/day reported in Stewart and Lavigne (1980).

We tested for differences in "maternal care" between years by selecting years with at least 30 pups aged 9 days or younger, and subjecting the logarithm of body mass (to remove heteroscedasticity) to a 2-way ANOVA (coat stage × year). Both factors were significant ($p < 0.0001$). However the interaction term was also significant, and body mass was not consistently low for all coat stages in

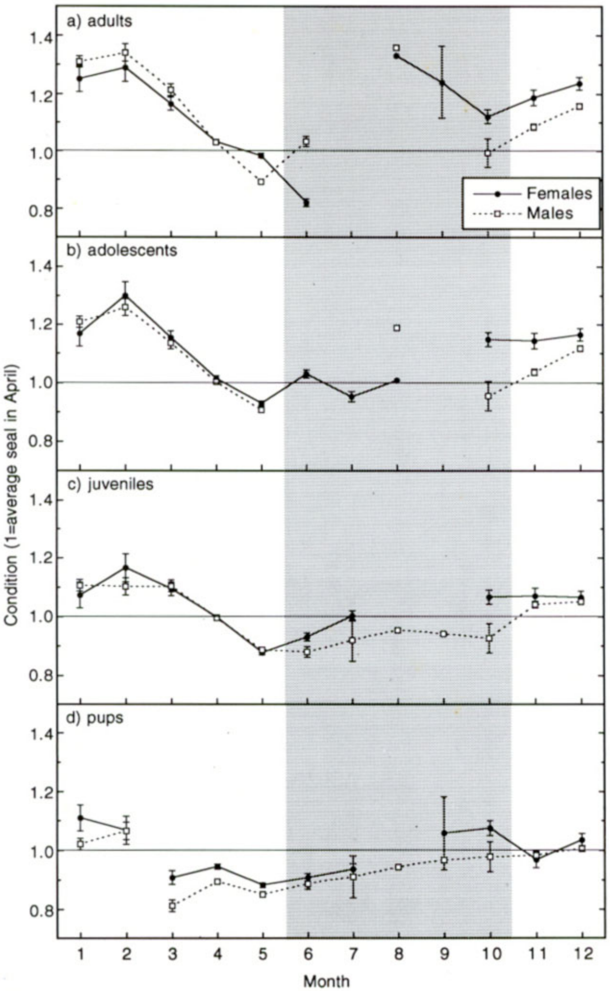

Fig. 12. Seasonal fluctuations in condition index (CI) for 4 age-classes of harp seals of both sexes. Details are as in Fig. 3.

any given year (Fig. 15). Although whitecoats were relatively light in 1983 and 1984, this analysis did not reveal a deterioration of neonatal growth with increasing population density. It is possible that the duration of each coat stage is affected by nutrition (Stenson, unpublished data), so that growth could indeed be decreased in years when resources are less available to the mother, without size achieved at the end of each stage being affected much.

Growth in length and mass of juveniles. Only juvenile (i.e. fast growing) seals (1–5 years) were selected for this analysis. Furthermore, to remove the variability due to seasonal fluctuations in L and M_t (see above), only seals sampled in April were selected. The study was divided into 4 periods of about 5 years. For each sex, an analysis of covariance was performed on L and another on M_t, with period as the factor and age as the covariate. The relationship between L or M_t and age was made linear by taking the square root of age, expressed in days (Trites and Bigg, 1992).

Females had different growth rates for L among the 4 periods ($F_{[3.1403]} = 3.21$, $p = 0.022$), and slower

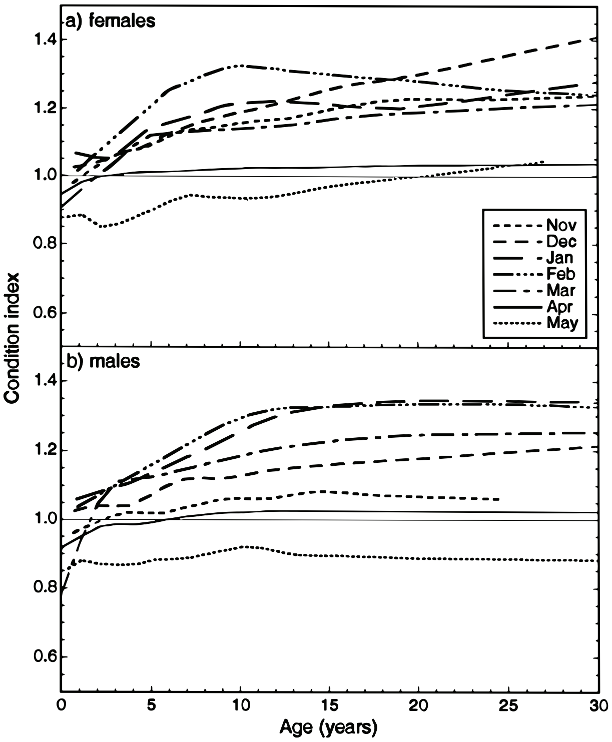

Fig. 13. Effect of age and season on the condition index (CI) of female and male harp seals. Fitted lines are as in Fig. 10.

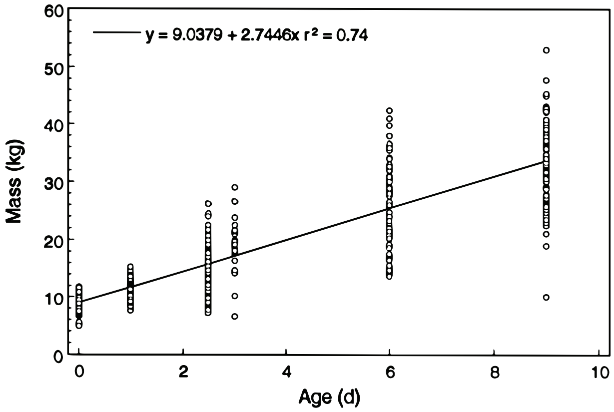

Fig. 14. Neonatal growth rate. Age was estimated by pelage type.

TABLE 5. Effect of seasonal changes in body length (L) on the magnitude of seasonal changes in condition index (CI) relative to changes in total body mass (M_t). Only adult seals are included.

Month	Sex	L	M_t	CI	% error	CI_c[1]
Feb	M	174.5	143.7	1.34		1.47
Apr	M	167.9	100.8	1.03		1.03
ratio Feb/Apr	M	1.04	1.43	1.30	-9.13	1.43
Feb	F	170.2	133	1.28		1.42
Apr	F	164.3	97.6	1.03		1.03
ratio Feb/Apr	F	1.04	1.36	1.24	-9.69	1.38

[1] Body length used in computation of CI_c for February was divided by 1.04 to estimate the length in April.

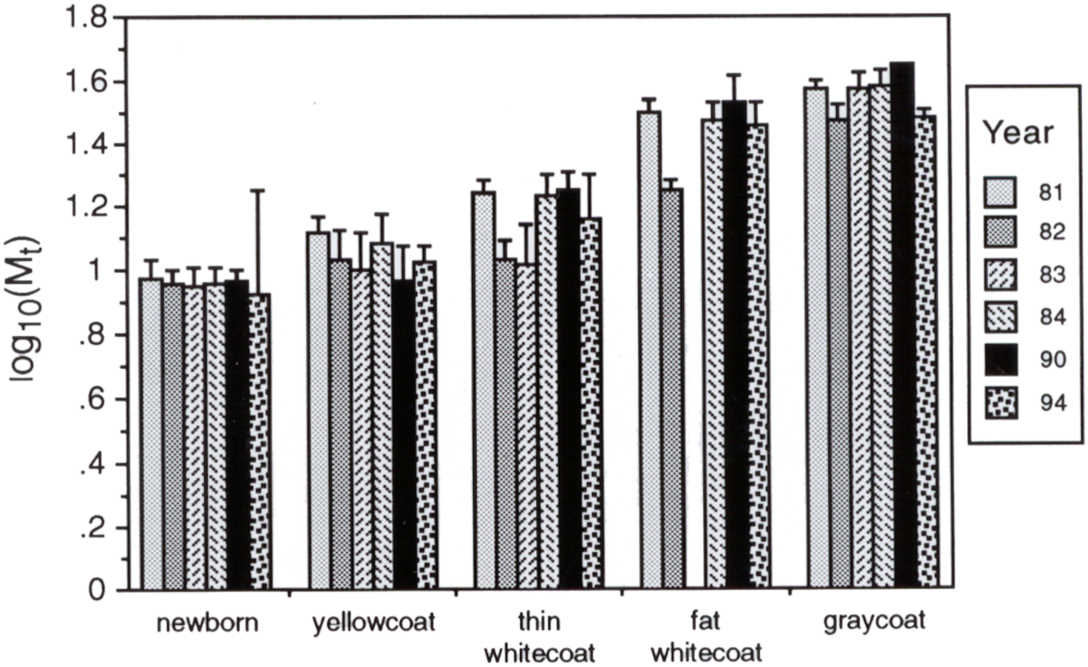

Fig. 15. Mean value and 95% condition index (CI) of body mass (M_t) (after logarithmic transformation) of harp seal pups by pelage type and by year. Only years with at least 30 pups aged 9 days or less were included.

growth rates were observed in the second half of the study period (Fig. 16, slope = 1.59, 1.50, 1.37 and 1.42 cm × $d^{-0.5}$ in 1976–79, 1980–84, 1985–89 and 1990–94, respectively). The results for growth in M_t were identical. Slopes differed among the study periods ($F_{[3.1127]} = 19.5$, $p < 0.0001$), declining as the study progressed (slope = 1.86, 1.64, 1.14 and 1.31 kg _ $d^{-0.5}$, but note the very small n in 1985–89). With males, growth rates for L ($F_{[3.1609]} = 1.45$, $p = 0.23$) as well as for M_t ($F_{[3.1305]} = 1.63$, $p = 0.18$) did not differ between the 4 periods (Fig. 17). However, multiple pairwise comparisons of adjusted means showed that males were significantly shorter (4–5 cm) and lighter (6–10 kg) in 1990–94 than in the previous 3 periods (again, note the small sample sizes in 1985–89).

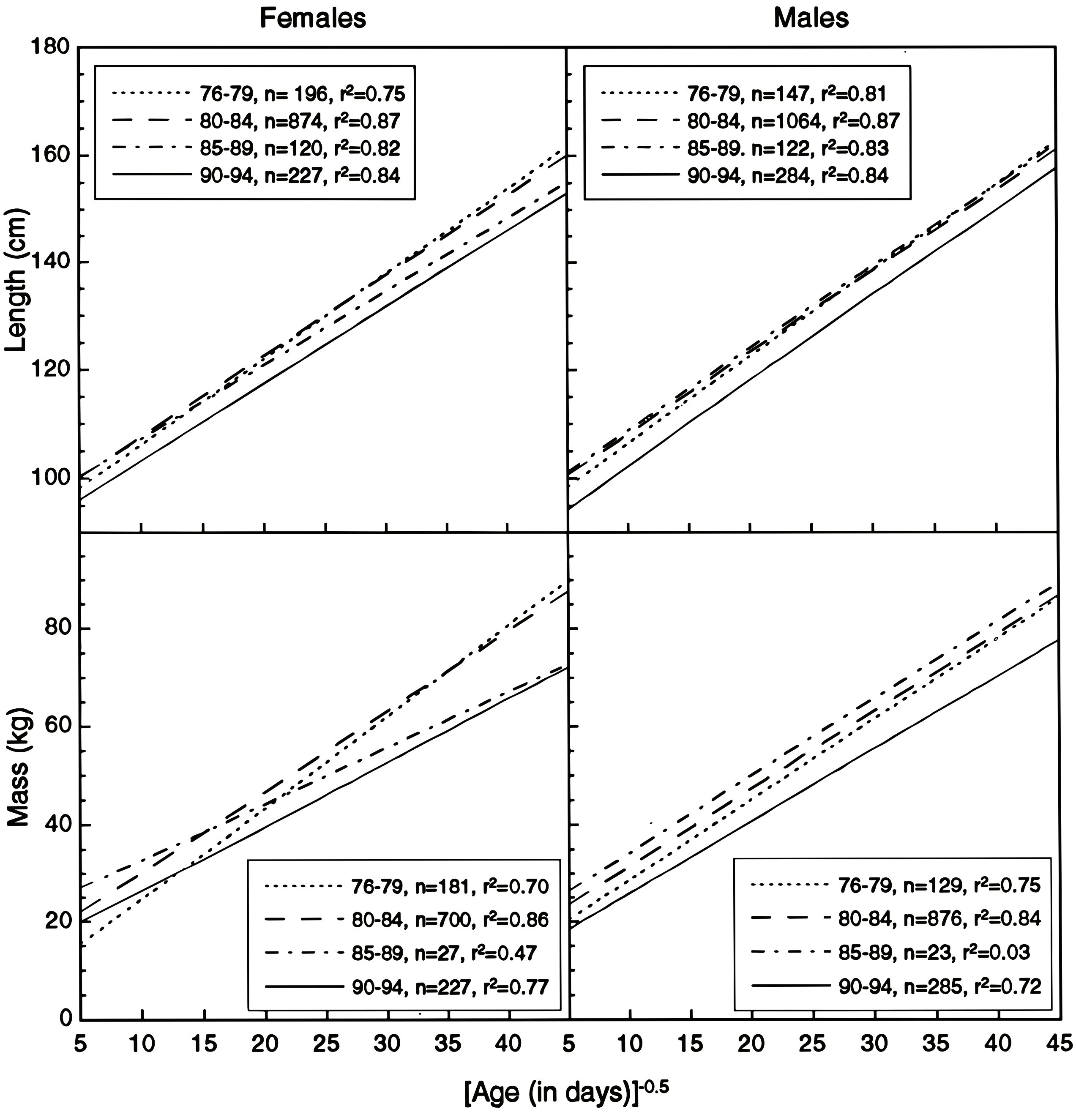

Fig. 16. Growth curves in standard length (L) and total body mass (M_t) of male and female juvenile harp seals during 4 time-periods.

Seals ≥5 years. Although adult seals have reached their final length (excluding seasonal fluctuations), they can be expected to have varying degrees of fatness depending on food availability. To increase sample size, we wanted to pool adolescent and adult seals. This precluded using W_t, which differed in the two age-classes. We used CI, which was independent of length for seals ≥110 cm or ≥5 years in April (Fig. 10 and 13). A 2-way ANOVA on CI (sex × year) was computed for seals ≥5 years sampled in April of the years for which n was large enough (1979, 1981, 1982, 1983, 1984 and 1992). The interaction term ($F_{(5.1261)}$ = 1.07, p = 0.37) and the sex effect ($F_{(1.1261)}$ = 1.59, p = 0.21) were not significant, but there was a year effect ($F_{(5.1261)}$ = 11.43, p <0.0001). Multiple comparisons

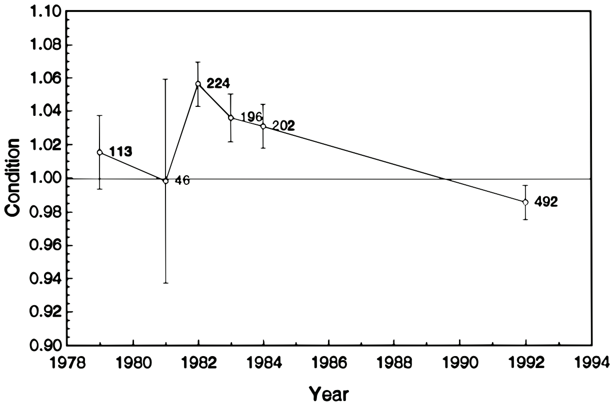

Fig. 17. Changes in condition index (CI) of harp seals ≥5 years between years. Means, 95% confidence intervals and sample sizes are displayed.

of means demonstrated that CI was significantly lower in 1992 than in 1982, 1983 or 1984 (Fig. 17), but not from 1979 (p was 0.0042, but p for significance with 15 comparisons was 0.0034), nor from 1981 (which had a small sample size). The only other significant difference was between 1981 and 1982.

Although no causal relationship was implied, we have demonstrated a reduction in growth rate or size-at-age for harp seals aged between 1 and 5 years occurring in recent years, when seal numbers had increased (Shelton *et al.*, 1996; Stenson *et al.*, 1996). Similarly, older seals were in poorer condition in 1992 relative to the period 1982–84. This decrease in condition in the early-1990s was paralleled by a decrease in pregnancy rate, and an increase in the mean age of sexual maturity in female harp seals (Sjare *et al.*, 1996). However, we found no differences in size or growth rates of seals during their first 9 days of life, although this conclusion would be invalidated if the relationship between coat pattern and pup age was affected by environmental conditions.

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