Changes in body growth of northern fur seals from 1958 to 1974: density effects or changes in the ecosystem?

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ABSTRACT

Analysis of morphometric measurements collected from northern fur seals (*Callorhinus ursinus*) between 1958 and 1974 suggests a periodicity in growth rates and physical condition that may reflect underlying, large-scale environmental changes. The data further suggest that fur seals attained larger body sizes as the breeding population on the Pribilof Islands declined over this 16-year period. These conclusions are based on changes observed in the mean body size and condition index of mature females, changes in the annual growth rates of immature females, and changes in male and female growth curves. Interpreting annual changes in physical growth is complicated by inconsistencies in sampling between years and by large natural variations in body mass and body length within years. Commercial fisheries may influence the abundance of prey, and alter the physical growth of pinnipeds, but other physical and biological factors are probably more important determinants. Changes in body length and mass are useful indicators of per capita prey abundance and offer useful insights into conditions experienced by fur seals. Unfortunately, it is not possible to determine whether changes observed in growth are due entirely to changes in population density or whether they reflect changes in the ecosystem, or some combination of both.

Key words: northern fur seals, physical growth, body length, body mass, growth curves, growth rates, condition index

INTRODUCTION

Changes in body growth may reflect changes in population density or changes in the ecosystem. Thus, Scheffer (1955) concluded that decreases in the body lengths of male northern fur seals (*Callorhinus ursinus*) during 1913–1920 and 1941–1952 were due to increased competition among seals for food around the Pribilof Islands, Alaska, which occurred as the population rose from its all-time low of 200,000 seals in 1910 to over 1.8 million in the late 1940s.

Population density remained high on the Pribilofs during the summer breeding season until the mid-1950s (Lander and Kajimura, 1982). However, between 1955 and 1970, the numbers of pups born on the Pribilof Islands dropped by 50% (York and Hartley, 1981; Trites and Larkin, 1989). In keeping with Scheffer's rationale, reduced intraspecific competition caused by the decline of the Pribilof fur seal population should have enhanced the growth of individual animals through the 1950s and 1960s.

The goal of our study was to use morphometric measurements recorded from seals shot at sea over the period 1958 to 1974 to test whether body size increased as the population declined. In addition to contemplating density effects, we also considered whether body growth might have been influenced by large-scale environmental factors.

METHODS AND RESULTS

The pelagic measurement data were collected from 1958 to 1974 by Canada (Department of Fisheries and Oceans) and the United States (National Marine Fisheries Service) under the auspices of the North Pacific Fur Seal Commission. A description of the procedures used to collect the fur seals along the west coast of North America (California to the Bering Sea), and the biases inherent in the data set are discussed in Lander (1980) and Trites (1990). Numbers of males, pregnant females, and non-pregnant females captured each month during the pelagic research program are con-

tained in Tables 1, 2, and 3. Exploratory data analysis was conducted with the S software package (Becker and Chambers, 1984) and statistical analyses were completed using BMDP statistical software (BMDP, 1988).

Northern fur seals of all ages experience seasonal increases and decreases in body mass and length related to the timing of migration and area of feeding (Trites, 1990). In general, rapid gains in mass and length occur during a brief 1–3-month period prior to the seals ar-

Table 1. Number of males collected at sea by month from 1958–1974.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan–Dec
1958	0	19	17	74	123	24	4	0	0	0	0	0	261
1959	10	8	23	44	16	14	0	0	0	0	0	0	115
1960	0	0	38	42	74	46	39	11	0	0	0	0	250
1961	8	7	67	74	33	6	0	0	0	0	0	0	195
1962	0	16	18	23	12	78	37	40	17	0	0	0	241
1963	0	0	0	3	8	14	57	51	4	0	0	0	137
1964	0	0	1	14	18	8	21	19	7	0	0	0	88
1965	0	0	0	29	6	3	0	0	0	0	0	0	38
1966	1	2	52	13	4	0	0	0	0	0	0	0	72
1967	7	6	2	6	5	0	0	0	0	0	0	1	27
1968	14	19	13	30	36	79	38	14	0	0	0	0	243
1969	0	13	22	27	30	0	0	0	0	0	0	0	92
1970	6	7	8	9	9	9	0	0	0	0	0	0	48
1971	2	3	20	14	29	0	0	0	0	0	0	2	70
1972	6	6	5	5	15	0	0	0	0	0	0	0	37
1973	0	0	0	0	0	0	16	39	19	0	0	1	75
1974	2	0	0	0	0	0	24	31	4	0	0	0	61
1958–1974	56	106	286	407	418	281	236	205	51	0	0	4	2050

Table 2. Number of pregnant and postpartum females collected at sea by month from 1958–1974.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan–Dec
1958	0	156	338	145	397	98	0	0	0	0	0	0	1134
1959	95	576	207	327	35	96	0	0	0	0	0	0	1336
1960	0	2	172	296	368	151	174	74	0	0	0	2	1239
1961	311	285	104	216	26	1	0	0	0	0	0	0	943
1962	0	32	3	16	47	333	176	309	109	21	0	0	1046
1963	0	0	0	0	12	113	278	555	19	0	0	0	977
1964	0	0	0	58	111	7	44	234	24	0	0	0	478
1965	0	0	0	88	62	35	0	0	0	0	0	0	185
1966	30	105	127	21	3	0	0	0	0	0	1	0	287
1967	41	26	0	17	5	0	0	0	0	0	2	45	136
1968	55	74	6	51	75	138	43	39	0	0	0	0	481
1969	0	52	88	40	33	0	0	0	0	0	0	0	213
1970	42	18	67	18	54	2	0	0	0	0	0	0	201
1971	48	3	88	48	28	0	0	0	0	0	0	11	226
1972	20	6	38	23	47	0	0	0	0	0	0	2	136
1973	22	8	0	0	0	0	151	166	139	0	0	3	489
1974	25	0	0	0	0	0	113	123	16	0	0	0	277
1958–1974	689	1343	1238	1364	1303	974	979	1500	307	21	3	63	9784

Table 3. Number of nonpregnant females collected at sea by month from 1958–1974.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan–Dec
1958	0	58	139	136	201	41	33	0	0	0	0	0	608
1959	33	184	134	169	46	20	1	0	0	0	0	0	587
1960	0	0	90	122	203	31	58	15	0	0	0	1	520
1961	135	108	147	236	76	6	0	0	0	0	0	0	708
1962	0	14	10	55	15	181	96	211	87	26	0	0	695
1963	0	0	0	5	18	66	112	291	6	0	0	0	498
1964	0	0	0	77	124	47	75	88	22	0	0	0	433
1965	0	0	0	114	66	58	0	0	0	0	0	0	238
1966	19	89	171	36	18	0	0	0	0	0	0	0	333
1967	32	19	8	30	27	1	0	0	0	0	1	36	154
1968	46	81	33	81	62	94	84	40	0	0	0	0	521
1969	0	57	102	62	98	0	0	0	0	0	0	0	319
1970	20	16	75	33	109	19	0	0	0	0	0	0	272
1971	40	14	74	70	78	0	0	0	0	0	0	12	288
1972	34	4	33	37	54	0	0	0	0	0	0	1	163
1973	11	1	0	0	0	0	23	57	65	0	0	2	159
1974	9	0	0	0	0	0	21	51	14	0	0	0	95
1958–1974	379	645	1016	1263	1195	564	503	753	194	26	1	52	6591

riving on the Pribilof Islands in July. During the rest of the year, as fur seals migrate from the Bering Sea to the coast of California, there is a gradual loss of body mass and length.

We controlled for seasonal effects by restricting growth comparisons to specific months and age classes. First, we constructed growth curves for seals collected over three consecutive periods of time. We then estimated the mean body size of mature, nonpregnant females collected each year from 1958 to 1974. Finally, we estimated the annual growth rate of immature females and determined the "condition" of those sampled.

Growth curves

Growth curves were plotted for year groups 1958–1962, 1963–1968, and 1969–1974 to compare changes that might have occurred over the period 1958–1974. The data were grouped to reduce possible biases associated with differences that occurred from one year to the next in population age structure and incomplete monthly samples (see Tables 1, 2, and 3). The first set of growth curves were drawn for immature males and females (aged 1.5–4.5 y). The second set of growth curves was drawn for pregnant and nonpregnant females (aged 5.5–15.5 y). In both cases, our analysis considered morphometric measures from the combined months of January through April because little or no seasonal change in body size occurs during this period,

which is prior to both the immature growth spurt and the rapid growth of fetuses carried by pregnant females (Trites, 1990, 1991).

The time-series of morphometric measures were smoothed by *lowess*, a nonparametric regression (Cleveland, 1979; Efron and Tibshirani, 1991), and visually compared. The lowess algorithm requires choosing a smoothness parameter f that is a number between 0 and 1. As f increases, the fitted curve becomes smoother. The standard error of the regression was estimated using a bootstrap procedure. For each lowess curve drawn in Figs. 1 and 2, 200 data sets of size n were drawn with replacement from each of the original data sets (see Table 4 for sample sizes n). For example, the 1958–1962 data set for immature females consists of 768 pairs of points. Two hundred data sets each consisting of 768 pairs of points were randomly drawn with replacement from this original data set. A lowess curve was fitted to each of these 200 data sets to estimate the length of seals aged 2, 3, and 4 years. Using the 200 estimates of length, the standard error was calculated for each age. This process was repeated for each of the 24 original data sets (Table 4).

The growth curves show an increase in the mass and length of immature males and females between 1958 and 1974 (Fig. 1). The same appears to be true for pregnant and nonpregnant females (Fig. 2). Confidence limits superimposed on each of the growth

Figure 1. Growth curves for immature males and females (ages 1.5–4.5 y) collected from January through April over three periods of time: A) 1958–1962, B) 1963–1968, and C) 1969–1974. The smoothed curves are nonparametric regressions (lowess, f = .60). The number of pairs of points fit with each regression is contained in Table 4. Confidence limits (95%) were calculated using a bootstrap procedure for ages 1.8, 2.8, and 3.8 years, but are barely discernable.
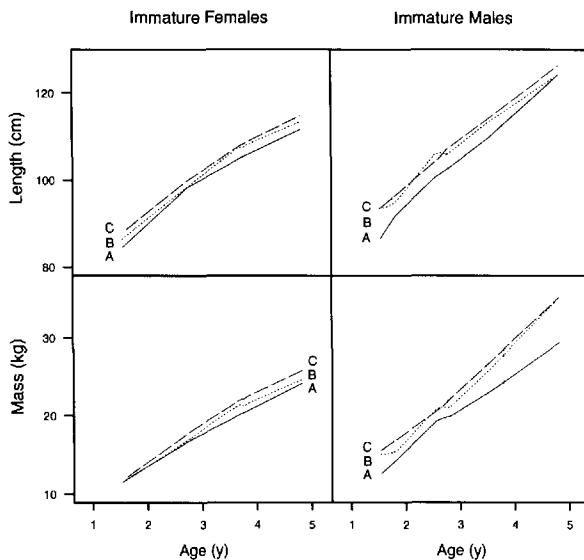
Figure 2. Growth curves for pregnant and non-pregnant females (ages 4.5+ y) collected from January through April over three periods of time: A) 1958–1962, B) 1963–1968, and C) 1969–1974. The smoothed curves are nonparametric regressions (lowess, f = .60). The number of pairs of points fit with each regression is contained in Table 4. Confidence limits (95%) were calculated using a bootstrap procedure for ages 7.8, 9.8, and 11.8 years, but are barely discernable.
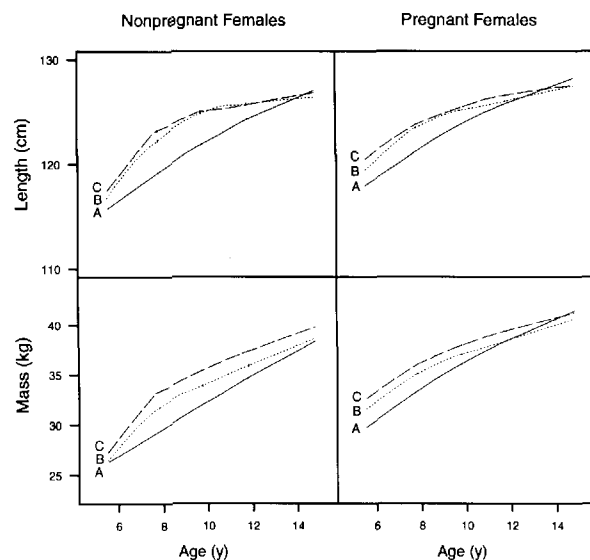

Table 4. Sample sizes for each of the lowess curves drawn in Figs. 1 and 2.

| | Immature | | Mature | | |
| | Females | Males | Non-pregnant females | Pregnant females | |
Years					Total
A. 1958–1962	768	198	507	2719	4192
B. 1963–1966	477	89	163	601	1330
C. 1967–1974	368	91	200	566	1225
Total	1613	378	870	3886	6747

curves are extremely tight due in part to the large sample sizes and the large f value used to smooth the data.

Fur seals seemed to be smaller during 1958–1962 compared with subsequent year groupings (Figs. 1 and 2). From 1963–1968 to 1969–1974, there was an increase in body mass, but virtually no difference in the body length of immature males and mature females. Perhaps the similarity of the length curves in the later years reflects a physiological maximum growth response to abundant food. The difference in body mass between years is marked and presumably means that seals became fatter with time (see Fig. 2).

In addition to fitting the morphometric data with nonparametric regressions, we also used linear regressions to compare growth rates. If no statistical difference was detected between the slopes, we compared the mean body size over the three year groupings by analysis of covariance (ANCOVA).

The relationship between length and age, and mass and age, for immature females were linearized by a square root transformation of age (measured in days). Growth rates (see body mass, Fig. 1, bottom left panel) increased from one year grouping to the next (0.71 to 0.77 to 0.81 kg $d^{-0.5}$) and were significantly different

from each other ($F_{2,1607} = 4.07$, $P = 0.017$). Body-length growth rates did not differ significantly between the three time periods ($F_{2,1607} = 0.39$, $P = 0.677$). The mean body lengths of immature females (adjusted by ANCOVA for differences in ages sampled) were 102.1, 104.0, and 105.0 cm for the grouped years ($F_{2,1607} = 36.73$, $P < 0.001$). Posthoc comparisons indicate that these differences between years were highly significant.

Between the ages of 1 and 5 y, male growth is nearly linear (Fig. 1, right panels). Growth rates did not differ significantly between the three periods of time (length: $F_{2,372} = 0.21$, $P = 0.809$; mass: $F_{2,372} = 0.04$, $P = 0.957$), but the adjusted group means did (length: $F_{2,372} = 18.55$, $P < 0.001$; mass: $F_{2,372} = 17.23$, $P < 0.001$). Posthoc comparisons revealed that immature males were significantly smaller in 1958–1962 than in the later year groupings. The immature male seals became progressively longer and heavier with time (length: 100.5, 103.6, and 105.1 cm; mass: 19.1, 20.5, and 21.9 kg). Only the difference in length between 1963–1968 and 1969–1974 was not significant ($t_{374} = 1.47$, $P = 0.14$).

The parametric tests support the conclusions drawn from the smoothed growth curves in Figs. 1 and 2: Mature and immature fur seals grew faster and attained larger body sizes as the Pribilof population declined through the 1960s and early 1970s.

Mean body size of mature nonpregnant females

We compared the mean length and body mass of mature nonpregnant females by year of collection. We only considered seals aged 14.5^+ y because annual growth increments and seasonal oscillations in body size are minor at this stage of their lives (Trites, 1990). We further pooled the data from all months of a given year because the sample sizes in some years were so small (i.e., only six seals sampled in 1967 were older than 14 y).

The mean length of mature seals captured from 1958 to 1974 should not have changed much over the course of a year because changes in length are largely a deterministic growth process. Furthermore, the year classes sampled overlapped from one year to the next, and were not completely independent of each other. Body mass, on the other hand, is probably a relatively plastic growth parameter that would vary more than length from one year to the next depending on the quality and quantity of food consumed.

Figure 3 supports the hypothesis that body length should not have changed significantly over the period 1958 to 1972. The coefficient of the linear regression fit to the raw data was not significant ($F_{1,678} = 0.71$,

Figure 3. Mean length and mass of mature non-pregnant females ages 14.5^+ y, collected from 1958–1974. The vertical bars are 95% confidence limits. The means were smoothed with locally weighted curves (lowess: $f = 0.60$).
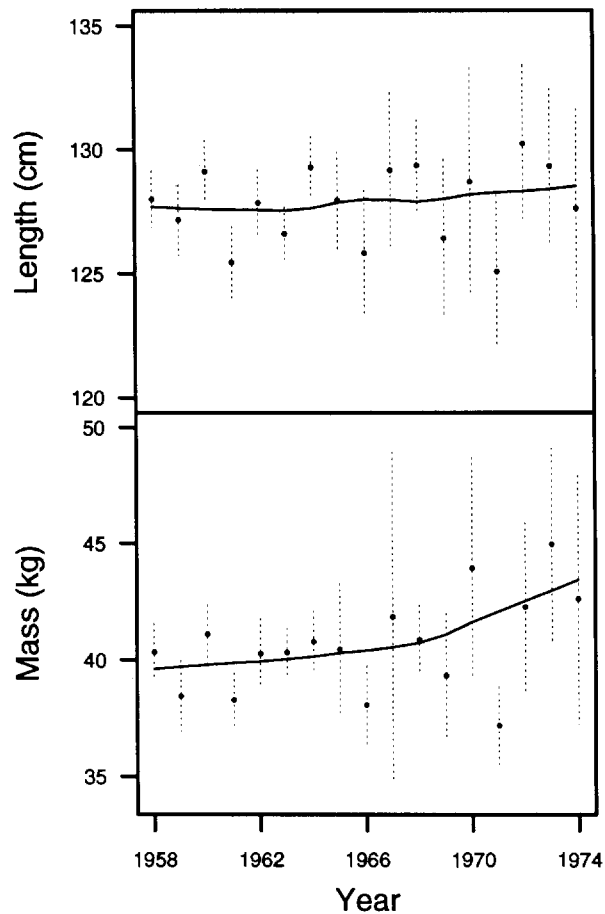
$P = 0.40$). But there was a positive change in body mass ($F_{1,678} = 5.17$, $P = 0.02$), suggesting that the mature females became heavier through the 1960s and into the 1970s.

Growth rates of immature females

The lengths and weights of females sampled before October were pooled for ages 1.5 to 4.5 y according to the year sampled. The morphometric measures were regressed against the age of the seals (measured in days) to estimate the annual growth rate. Confidence limits were determined for the slope (growth rate) of each regression according to Zar (1984).

The analysis was done by year of collection and not by year-class because body size varies seasonally and the months sampled were not the same each year (see Table 3). For example, if 2-year-olds were sampled in

April before the growth spurt, and 4-year-olds were sampled two years later in July after attaining their maximal seasonal size, the estimated growth rate would be positively biased. Growth rates by year-class can only be calculated and compared if the months of sampling are standardized, which was not possible given the pelagic sampling design.

Growth rates of seals sampled in any given month of the year should be the same despite the seasonal fluctuations in body size. For example, if body length measured in April is regressed against age, the slope (but not the intercept) should be similar to the regression coefficient for samples from another month, such as July. We tested this by analysis of covariance.

Selecting any given year (e.g., 1962), we compared the mean size of the immature seals caught each month (i.e., June, July, August, and September) after adjusting for age and testing whether the monthly growth rates were significantly different from one another (BMDP, 1988). We found that the adjusted group means of the 1962 samples differed (length $F_{3,236}$ = 5.91, P = 0.001 and mass $F_{3,236}$ = 9.08, $P < 0.001$), but could not detect a significant difference between the monthly growth rates (length $F_{3,236}$ = 0.95, P = 0.42, and mass $F_{3,236}$ = 1.03, P = 0.38). We repeated this for two additional years (1961: Feb–May; 1968: Apr–Jul) where we felt sample sizes were sufficiently large. Again, the monthly growth rates did not differ, but the adjusted mean sizes did. Thus, we felt it reasonable to compare the growth rates by year of collection because the slopes within a year did not appear to differ significantly.

Figure 4 shows the annual growth rates of immature females from 1958 to 1974. There is some suggestion of a periodic change in growth rates for body length, which declined to their lowest value in 1962, peaked in 1968, and declined thereafter. Growth rates for body mass also peaked in 1968 but show no signs of having changed through the late 1950s and early 1960s.

We were concerned that the differences in growth rates between years might be an artifact of population age structure. Perhaps the estimated growth rates depend on the relative numbers of 2-, 3-, and 4-year-olds sampled. We checked this by taking Monte Carlo samples, consisting of equal numbers of each age group, and found that the growth rates estimated by repeated sampling were virtually identical to those shown in Fig. 4.

These results give a much finer resolution of changes in growth than do the three year-grouped growth curves drawn in Fig. 1. We believe the year-grouped growth curves failed to detect the low growth

Figure 4. Growth rates of immature females. The lengths and weights of seals aged 1.5 to 4.5 y were pooled by year of collection, then plotted against their age (in days) and fit with linear regressions. The slope of each regression (the growth rate) is shown with 95% confidence intervals. The time series of growth rates were smoothed with locally weighted curves (lowess: f = 0.40).
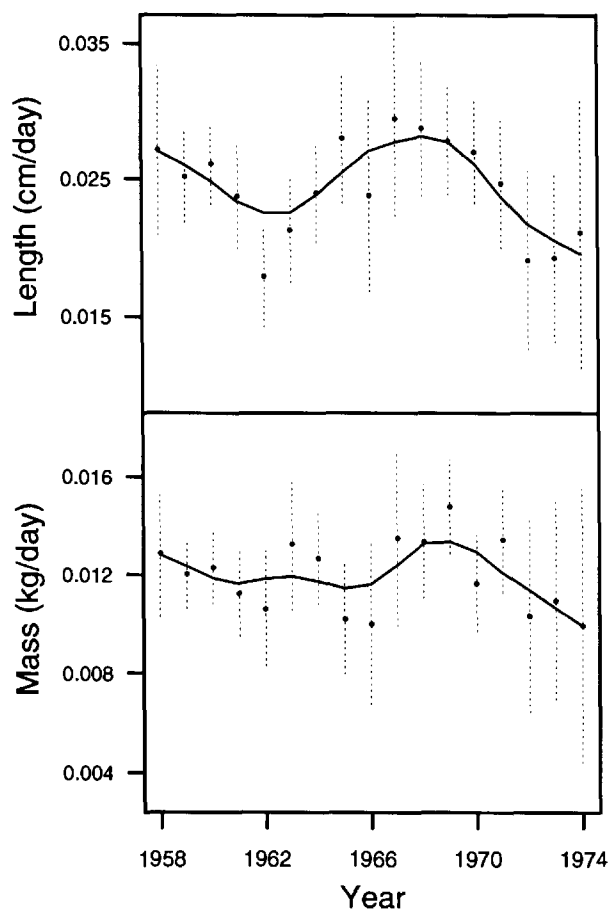
rates in the early 1960s and early 1970s because the number of seals sampled during these years from January to April were few or none at all (see Table 3). Note, however, that Fig. 4 deals only with growth rates and infers nothing about changes in mean body size.

Condition indices

The physical condition of a single seal was quantified with a condition index (CI) defined as the ratio between recorded mass (M) and expected mass ($\hat{M}$) where

$$CI = \frac{M}{\hat{M}}. \tag{1}$$

The expected mass of mature nonpregnant females was estimated from the empirical relationship between body length (L) and mass of nonpregnant females: $\hat{M}$ = 6.08 × $10^{-5} L^{2.74}$ (from Trites, 1990). The condition index of immature females was calculated from the allometric relation $\hat{M}$ = 2.055 × $10^{-4} L^{2.469}$ derived for seals between the ages of 1.5 and 4.5 y (n = 2,753).

The mean condition for all mature or immature fur seals is 1.0 (all years combined). However, between years (see Figs. 5 and 6), the mean condition falls about the grand mean (CI = 1.0) depending on whether conditions in any given year were "good" (CI > 1.0) or "bad" (CI < 1.0). The terms "good" and

Figure 6. Mean condition of mature nonpregnant females aged 14.5[+] y collected from 1958–1974. The vertical bars are 95% confidence limits. The positive relationship between condition and time is described with a simple linear regression ($F_{1,678}$ = 4.29, P = 0.04).

Figure 5. Mean conditions of immature females by year of collection. Each data point indicates the age group (2: 1.5–2.5 y; 3: 2.5–3.5 y; 4: 3.5–4.5 y). In the top panel, the alternating dashed and solid lines join the mean condition of each age group by year-class. In the bottom panel, the mean condition is smoothed by age group (lowess f = 0.60). The top and bottom lines were fit to ages 4 and 2 y, respectively. The center dashed line is for age 3 y.
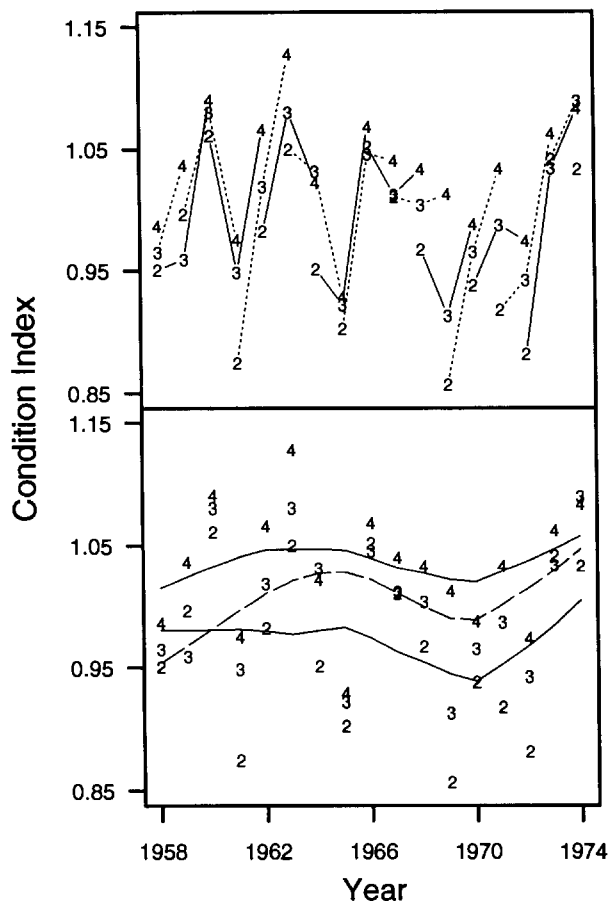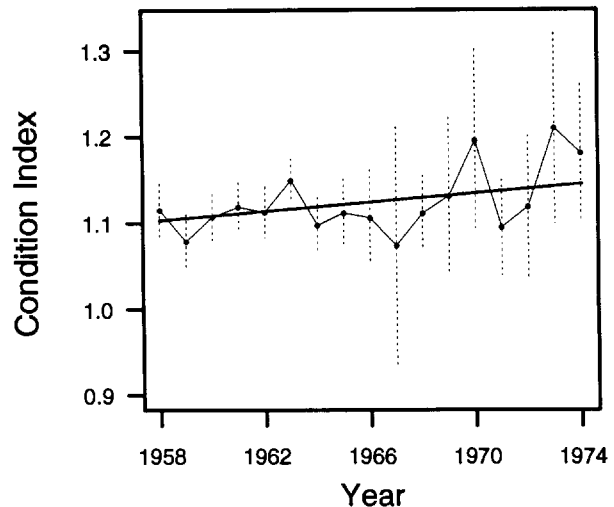

"bad" are relative, not absolute. For example, the entire population may have experienced poor conditions from 1958 to 1974, but some years may have been better or worse than others.

The effect of age on condition appears to predominate more than annual effects. For example, the condition of females improves with age (Figs. 5, bottom panel, and 6), but does not change in a clearly discernible way with time (1958 to 1974). A linear regression fit to the condition of nonpregnant females aged 14.5[+] years over time (Fig. 6) suggests that there was a general improvement in body condition ($F_{1,678}$ = 4.29, P = 0.04). But the condition of immature females (Fig. 5) may have declined from 1963 to 1972.

There is a tendency for mean condition indices of different age classes to be clustered within a year, but to vary markedly between years (Fig. 5, top panel). Furthermore, condition appears to vary from year to year independently of the cohort.

DISCUSSION

It was not possible simply to compare fur seal growth in the late 1950s (when the population was relatively high) to growth at low abundance during the 1970s. A straightforward analysis was precluded by inconsistencies in sampling during the 1958 to 1974 pelagic research program. For example, fur seals were sampled in different areas of the north Pacific in different years. In

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