

Reevaluating evidence of density-dependent growth in northern fur seals (*Callorhinus ursinus*) based on measurements of archived skeletal specimens

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Abstract: Analysis of length-at-age measurements of archived skeletal material shows that somatic growth rates of male northern fur seals (*Callorhinus ursinus*) vary inversely with population density. Von Bertalanffy growth curves were estimated for two series of known-age mandibles collected 1911–1920 ($n = 156$) and 1940–1953 ($n = 151$), time periods representing the historic population minimum and maximum, respectively. Mandibles from the former time period are larger than mandibles from the latter time period, suggesting a density-dependent response in somatic growth. Although density-dependent growth in northern fur seals has been suggested before, previous studies have been hampered by the potentially confounding factors of fisheries interactions, variable environmental conditions, and harvest of adult female northern fur seals. The material analyzed here pre-dates the substantial development of the Bering Sea groundfish fishery and the period of heaviest culling of females. Likewise, the two time periods examined are characterized by broadly similar climatic and environmental conditions. Therefore, the results support the hypothesis that measurements of somatic growth rates provide an index of population levels relative to carrying capacity. Growth rate studies could therefore be used to evaluate the current population status of northern fur seals.

Résumé : L'analyse des mesures de longueur en fonction de l'âge faites sur des os de l'otarie à fourrure du nord (*Callorhinus ursinus*) conservés en musée montre que la croissance somatique des mâles est inversement proportionnelle à la densité de la population. Nous avons estimé les courbes de croissance de von Bertalanffy pour deux séries de mandibules d'âge connu récoltées en 1911–1920 ($n = 156$) et en 1940–1953 ($n = 151$), des périodes qui correspondent respectivement au minimum et au maximum de densité de la population dans le passé connu. Les mandibules de la première période sont plus grandes que celles de la seconde, ce qui laisse croire à une réaction de dépendance de la densité dans la croissance somatique. Bien qu'on ait dans le passé indiqué que la croissance des otaries à fourrure est liée à la densité, les études antérieures sont embrouillées par la présence de facteurs confondants comme les interactions avec les pêches, les conditions variables de l'environnement et la récolte d'otaries à fourrure femelles. Le matériel que nous avons analysé a été récolté avant l'important développement des pêches commerciales des poissons de fond dans la mer de Béring et avant la période d'élimination maximale des femelles. De plus, chacune des périodes examinées se caractérise par des conditions climatiques et environnementales généralement similaires. Les résultats appuient donc l'hypothèse selon laquelle les mesures de croissance somatique fournissent un indice des densités de la population relativement au stock limite. Des études de taux de croissance pourraient servir à évaluer le statut actuel des populations d'otaries à fourrure du nord.

[Traduit par la Rédaction]

Introduction

Between the early 1950s and the 1970s, the population of northern fur seals (*Callorhinus ursinus*) in the Pribilof Islands, Alaska, declined approximately 60% (York and Kozloff 1987; York 1990; Sinclair et al. 1994). This decline is thought to have been caused primarily by direct take of adult females (York and Hartley 1981), a practice that was most prominent from 1958 to 1974. The Pribilof Islands popula-

tion stabilized from 1981 to 1995 at a level considered to be "depleted" under the Marine Mammal Protection Act (United States Code 1972; Angliss and Lodge 2004) and has declined at a rate of 6% per year since 1998 (NMML 2004). Current management interests are aimed at understanding the various mechanisms that may have caused this stabilization and subsequent decline. One of the mechanisms that has received considerable attention is density-dependent regulation of vital rates such as mortality, survival, and growth

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(Fowler 1990). The research presented here expands on previous efforts to understand variability in somatic growth rate as a function of population level through the analysis of archived skeletal material collected 1911–1953 (for the use of other such indices see Swartzman and Haar 1983; Fowler and Siniff 1992). If the reaction of growth response of northern fur seals, hereinafter referred to as fur seals, to variability in population level can be accurately modeled, biologists will have a valuable tool for evaluating current population status and predicting future population trends (following the approach suggested by Fowler and Siniff 1992).

Somatic growth rates of fur seals have long been known to correlate inversely with population levels (Scheffer 1955), and this model has been refined through subsequent analyses (Baker and Fowler 1990; Fowler 1990; Trites and Bigg 1992). However, each of these studies utilizes different data (Table 1), making comparison of the results difficult. Furthermore, although variability in per capita food availability is clearly implicated, it is not clear if this correlation reflects changes in the abundance of prey items, the abundance of fur seals, or both (Trites and Bigg 1992).

The present study attempts to clarify the issue by utilizing measurements of archived skeletal material collected during two of the most noteworthy time periods of fur seal population history in the 20th century: 1911–1920, when the fur seal population was at its historic low of between 200 000 and 300 000 individuals, and 1940–1953, when the fur seal population had stabilized at its historic high of around 1.5 million (Lander 1980; York 1987). Hereinafter I will refer to these two time periods as *popmin* and *popmax*, respectively. Importantly, both of these time periods pre-date the development of extensive commercial fishing in the North Pacific Ocean/Bering Sea (Swartzman and Haar 1983; Trites and Bigg 1992, 1996). Thus, any variability in growth rates during these two time periods should be related primarily to variability in the abundance of fur seals rather than to fisheries-induced variability in the abundance of prey items (assuming no major oceanographic changes occurred over these time periods: see Discussion below). Furthermore, both *popmin* and *popmax* pre-date the period of extensive culling of adult females (1958–1974), which has been blamed for the population decline of the fur seal herd in the latter half of the 20th century (York and Hartley 1981). If variability in growth rates of fur seals is controlled primarily by population levels (coupled with feedback loops that “cascade” through the ecosystem; Estes 1996), then individuals collected during *popmin* are expected to grow faster and (or) to a larger overall size than individuals collected during *popmax*.

Numerous researchers have attempted to document density-dependent somatic growth in northern fur seals. In spite of the wide variety of data sets that have been employed, each of the studies detailed below has limitations related to sampling. Scheffer (1955) presented the first analysis of density-dependent growth in fur seals. The time periods represented in his study were 1913–1920 and 1941–1952, essentially the same as those covered by the present study. However, in his analysis Scheffer used mean measurements of length, weight, skull length, and skull width for discrete age classes (summarized in Table 1) and then compared means between time periods. This approach limited Scheffer to comparisons be-

tween four discrete age classes (3- to 6-year-old males) for the length and weight data, and only two age classes (5- and 6-year-old males) for the skull measurements. Nevertheless, Scheffer's data suggested that growth rates were lower during the population plateau (1941–1952) than during the population low (1913–1920).

Fowler's (1990) research on density-dependent growth in fur seals utilized a substantially different data set than Scheffer's to evaluate the same process. During the time period 1958–1974, 2050 males and 16 375 females were killed during pelagic research cruises for scientific study under the auspices of the North Pacific Fur Seal Commission (Lander 1980). Using data from these research cruises, Fowler (1990) regressed body size against pup production (as an index of population size) for 19 discrete age classes of females. Seventeen of those age classes showed significant negative correlation between body size and pup production.

Although it would seem that the question of whether or not fur seals display density-dependent growth has been abundantly supported in the affirmative, Trites and Bigg (1992, 1996) have challenged this interpretation on a number of grounds. The first is that studies based on the pelagic sampling of 1958–1974 mask significant seasonal fluctuations in measurements of body size (both mass and length) of adult female fur seals (Trites and Bigg 1992, 1996). When these seasonal fluctuations are taken into consideration, body size still shows a significant negative correlation with population level for the time period 1958–1974 (Trites and Bigg 1992). However, the latter years of this time period also coincide with unparalleled development of the commercial groundfish fishery in the eastern North Pacific and Bering Sea (Bakkala 1993). Trites and Bigg (1992) agree that the ultimate cause of variability in growth rates is related to per capita availability of food. But because the development of commercial fishing coincides with declines in the fur seal population, the effects of the two variables may be confounded for samples collected after the 1960s (Trites and Bigg 1992). Finally, Trites and Bigg (1992) point out that none of the previous studies effectively evaluates the role of climatic variability as regards per capita prey availability for fur seals.

Considering the merits and limitations of the previous studies, an approach that combines aspects of all of these previous studies is warranted. Because of the possible confounding factors of large-scale commercial fishing and the harvests of adult female fur seals, samples should pre-date the 1960s. Likewise, an index of body size is needed that has low measurement error and minimal seasonal fluctuation above and beyond the general trends in growth. Finally, an analytical approach that can utilize data from continuous, rather than discrete, age data will help account for variability in the season in which specimens were collected. Length-at-age data of archived skeletal material collected throughout the first half of the 20th century meet these criteria, and will be used to generate growth curves to evaluate if fur seals demonstrate density-dependent growth.

Materials and methods

This study utilizes measurements of the mandibles from skeletal specimens archived in the research collections at the

Table 1. Data sets and time periods that have been the focus of previous attempts to document density-dependent growth in northern fur seals.

Study	Time period	Rationale	Measurement used	Age classes	Sample size
Scheffer 1955	1913–1920	Population low	Length	3- to 5-year-old males	214
			Weight	3- to 6-year-old males	248
Scheffer 1955	1941–1952	Population high	Skull length	5- and 6-year-old males	29
			Skull weight	5- and 6-year-old males	27
			Length	3- to 5-year-old males	4 753
			Weight	3- to 6-year-old males	211
Fowler 1990	1958–1974	Population declining	Skull length	5- and 6-year-old males	32
			Skull weight	5- and 6-year-old males	33
			Length vs. population	19 categories, females	16 375
Baker and Fowler 1990	1948–1984	Population fluctuating	Length vs. population	2 categories, males	5 050
			Weight vs. population	19 categories, females	16 375
			Weight vs. population	2 categories, males	5 050
			Tooth weight vs. population	3-year-old males	14 286
Trites and Bigg 1992	1958–1962	Equal time periods	Mass and length	4-year-old males	7 852
				1.5- to 4.5-year-old males	198
This study	1911–1920 1940–1953	Population low Population high	Mandible length Mandible length	1.5- to 4.5-year-old females	768
				5.5- to 15.5-year-old females	3 226
				1.5- to 4.5-year-old males	89
				1.5- to 4.5-year-old females	477
				5.5- to 15.5-year-old females	764
				1.5- to 4.5-year-old males	91
				1.5- to 4.5-year-old females	368
				5.5- to 15.5-year-old females	766
				0- to 8-year-old males	156
				0- to 11-year-old males	151

National Museum of Natural History in Washington, D.C., and the National Marine Mammal Laboratory in Seattle, Wash. In most cases these specimens were collected specifically for age-determination studies (Osgood et al. 1915; Scheffer et al. 1984). For the time period 1911–1920 (popmin), 156 mandibles were collected representing cohorts born in 1908–1918 (Table 2). For the time period 1940–1953 (popmax), 151 mandibles were collected representing cohorts born in 1937–1953. These time periods are delineated primarily by the collection years of known-age specimens and by population trends (Osgood et al. 1915; Scheffer et al. 1984). The upper limit of the latter time period marks the beginning of the substantial harvesting of females — a practice that is blamed for the precipitous decline of the fur seal population in the late 1950s and early 1960s (York and Hartley 1981; Trites 1992a). As in all of the studies outlined above, this analysis will utilize cross-sectional rather than longitudinal data to estimate somatic growth rates.

The use of skeletal measurements has numerous advantages over approaches taken in previous studies. First, bone length is strongly correlated with body size (Scheffer 1950b; Scheffer and Wilke 1953). Consequently, bone measurements from known-age specimens provide an index of variability in somatic growth rate for each of the different time periods. Second, although the activity of osteoclasts and the rate of bone remodeling may vary by season, bone length is not expected to exhibit seasonal fluctuation to the same degree as body weight and body length (Trites and Bigg 1992, 1996), thus reducing the amount of background noise anticipated in the data set. A third advantage to using skeletal measurements is that such measurements are easily standardized, thereby minimizing measurement error. Fourth, the results of this study are easily replicable, with the possibility of verifying the age of any outliers by sectioning a canine tooth (Scheffer 1950b). Perhaps most importantly, the specimens utilized for this study were collected during the historic population low and high points. The data utilized here therefore hold the promise of showing the maximum expected differences in growth patterns of any time period in the 20th century. Furthermore, limiting my analysis to the time periods 1911–1920 and 1940–1953 eliminates two of the confounding factors identified by Trites and Bigg (1992) that have hampered other such studies: the substantial development of the pollock (*Theragra chalcogramma*) fishery and the harvest of adult female fur seals.

For the purposes of this study, age has been calculated in fractions of years. Although the annual average date of birth has been shown to vary between 3 and 11 July, depending on the year and analytical methods used (Trites 1992b; Gentry 1998), I have used Peterson's (1965) estimate of 7 July as the average day of birth to define zero age. I assume that the collection date is synonymous with the date of death of the individual. Given the remarkably synchronous birthing behavior of fur seals (75% of all births occur within a 3-week period; Trites 1992b), and the fact that the majority of the specimens studied here were collected specifically for age-determination studies, the calculated ages are not likely to be more than 1 or 2 months in error. However, a few individuals utilized in this study were aged via external examination of the upper canine (following Scheffer 1950a). This aging technique has a high degree of accuracy, with approxi-

mately 99% of age estimates falling within 1 year of the correct age (Anas 1970). Error rates in age determination are assumed to be similar for the two time periods considered here and should not bias the results significantly (Leberg et al. 1989).

Measurements were taken on the mandible of known-age male specimens. The specific measurement used here is termed mandibular short length (MSL) and is defined as the distance from the posterior margin of the last post-canine to the lateral margin of the mandibular condyle, measured on the lateral aspect of the mandible (Parkington 1972; Woodborne et al. 1995). MSL was measured to the nearest 0.01 mm on right mandibles when present, using digital calipers. In the absence of the right mandible, the left was used. A series of 361 paired mandibles was measured to evaluate any differences in MSL between sides. No significant difference between the two sides was found (paired $t = -0.124$, $p = 0.901$). Thus, the left mandible can be reliably used for this analysis in the absence of the right mandible.

The relationship between MSL and age was characterized by a von Bertalanffy (VB) growth curve (von Bertalanffy 1938, 1960) for each time period using nonlinear parameter estimation in SPSS (Norusis 1998). Although VB growth curves are most often found in the fisheries literature (Fabens 1965; Kimura 1980; Schnute 1981), their general applicability to length-at-age data makes them ideally suited for analyses of this type (McLaren 1993; Winship et al. 2001; but see also Day and Taylor 1997).

VB growth curves consist of a three- or sometimes four-parameter equation of the form

$$(1) \quad Y(t) = y_{\infty}[1 - e^{-g(t-t_0)}]^p$$

where $Y(t)$ represents size at age t , y_{∞} is the asymptotic maximum size, g represents the rate at which size approaches the asymptote, t_0 is the age at which size is zero, and p describes the shape the curve takes as it approaches the asymptote.

One of the limitations of using the VB growth equation as formulated above is that it is often the case that nonlinear parameter estimation based on a minimization of the sums of squares fails to converge on an optimum solution (Schnute 1981). As a means of bypassing this problem, Schnute (1981) has developed a series of equivalent equations with parameters that have stable statistical estimates. Of the several equations presented by Schnute (1981), that which is most appropriate here is

$$(2) \quad Y(t) = \left[y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-T_1)}}{1 - e^{-a(T_2-T_1)}} \right]^{1/b}$$

Once again $Y(t)$ represents size at age t , but in this equation T_1 and T_2 are specified a priori and represent the youngest and oldest ages over which growth rates are to be calculated. Thus, four parameters remain to be estimated. Parameters a and b are equivalent to g and $1/p$, respectively, from eq. 1. That leaves y_1 and y_2 , the estimated average size at ages T_1 and T_2 , respectively. In addition to providing stable parameter estimates more reliably than eq. 1, eq. 2 eliminates the need to choose one of the several possible growth functions to describe a data set (Knight 1968; Ricker 1979; Schnute 1981). Furthermore, the parameters estimated for eq. 2 can

Table 2. Age distribution of sample by cohort year.

Cohort year	Age of specimen at time of collection (years)												Cohort total
	Pup	1	2	3	4	5	6	7	8	9	10	11	
1908	—	—	—	2	—	—	1	—	—	—	—	—	3
1909	—	—	2	—	—	—	—	—	—	—	—	—	2
1910	—	—	—	—	7	—	—	—	—	—	—	—	7
1911	3	—	—	37	—	1	5	1	—	—	—	—	47
1912	—	—	14	8	20	6	3	29	6	—	—	—	86
1913	—	—	—	—	1	—	—	—	—	—	—	—	1
1914	2	—	—	—	—	—	—	—	—	—	—	—	2
1915	—	—	—	1	—	—	—	—	—	—	—	—	1
1916	1	4	1	—	—	—	—	—	—	—	—	—	6
1918	1	—	—	—	—	—	—	—	—	—	—	—	1
1937	—	—	—	1	—	—	—	—	—	—	—	—	1
1938	—	—	—	—	—	—	—	—	—	1	—	—	1
1939	—	—	—	—	—	—	—	—	1	—	—	—	1
1940	1	10	—	—	14	12	—	—	—	1	1	—	39
1941	2	1	—	24	2	2	21	6	4	—	2	1	65
1942	—	—	—	—	—	—	—	—	—	—	1	—	1
1943	—	—	—	1	—	—	—	—	—	—	—	—	1
1945	2	—	—	—	—	3	—	—	—	—	—	—	5
1946	—	—	—	1	4	—	—	—	—	—	—	—	5
1947	2	2	—	10	—	—	—	—	—	—	—	—	14
1948	—	—	9	—	—	1	—	—	—	—	—	—	10
1949	3	2	—	—	—	—	—	—	—	—	—	—	5
1950	—	1	—	—	—	—	—	—	—	—	—	—	1
1951	—	1	—	—	—	—	—	—	—	—	—	—	1
1953	1	—	—	—	—	—	—	—	—	—	—	—	1
Age class total	18	21	26	85	48	25	30	36	11	2	4	1	307

Note: The collection year can be determined by adding the age at time of collection to the cohort year (i.e., the 1908 cohort collected as 3-year-olds was collected in 1911).

be used to calculate y_{∞} and t_0 if they exist (which will not always be the case; see Schnute 1981).

The expectations of the hypothesis of density-dependent growth can be linked directly to the VB growth curve. As discussed above, individuals sampled during the historic population low (popmin) are expected to grow faster and (or) to a larger overall size than individuals from the historic population high (popmax). This can be evaluated in an approximate way by comparing individual parameter estimates (Kimura 1980) or by simultaneously comparing all of the parameters within the full VB growth curve model.

Results

Individuals available for this analysis ranged in age from pups to adults 11 years of age (Figs. 1 and 2; Table 2). The age distribution of the samples has two important consequences for this analysis. The first is that although individuals at either extreme of the age distribution contribute to the overall solution of the parameter estimation, the growth curves for the two time periods are only comparable between 0.0 and 8.0 years of age (e.g., T_1 and T_2). While this age range encompasses most male fur seal growth, growth continues at a decreasing rate until the 10th year or so (Scheffer 1950b; Scheffer and Wilke 1953). Older individuals were collected during these time periods. However, external examination of the canines is not an effective way of

estimating the age of animals older than 7–8 years (Scheffer 1950a). Consequently, they have been identified only as “adult” or “>10 years old”, and have been omitted from this analysis. The second consequence of the age distribution is that because the samples do not cover the entire period of growth, no solution for asymptotic size (y_{∞}) exists for either cohort (Schnute 1981).

Keeping these limitations in mind, I plot MSL against age for each of the two time periods separately with the corresponding VB growth curves (Figs. 1 and 2). In spite of the fact that no solution for y_{∞} can be calculated, the growth curves for the two time periods differ in the manner predicted under the hypothesis of density-dependent growth (Fig. 3): individuals sampled during popmin grew more quickly and (or) to an apparently larger size than during popmax. In point of fact, the two terms describing the shape of the growth curves (a and b) for each cohort are statistically indistinguishable (Table 3). Likewise, the estimates of y_1 (i.e., size at age $T_1 = 0.0$) are also statistically indistinguishable. However, the estimate of y_2 (i.e., size at age $T_2 = 8.0$) is significantly higher for popmin than for popmax (F ratio for equivalence of variance = 1.90, $p < 0.001$; Welch's $t = 3.75$, $p < 0.001$).

Before these results can be interpreted in terms of fur seal population levels, the available information on climatic variability in each of the two time periods needs to be evaluated, as advocated by Trites and Bigg (1992). As they point out,

Fig. 1. Scatter plot of length-at-age data for mandibles from male northern fur seals (*Callorhinus ursinus*) collected between 1911 and 1920 ($n = 156$), with the corresponding von Bertalanffy growth curve.

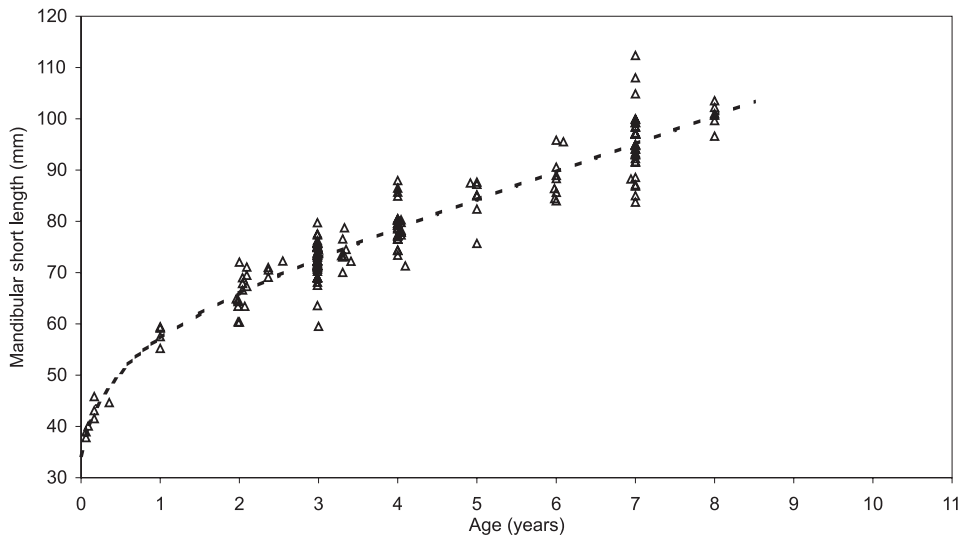
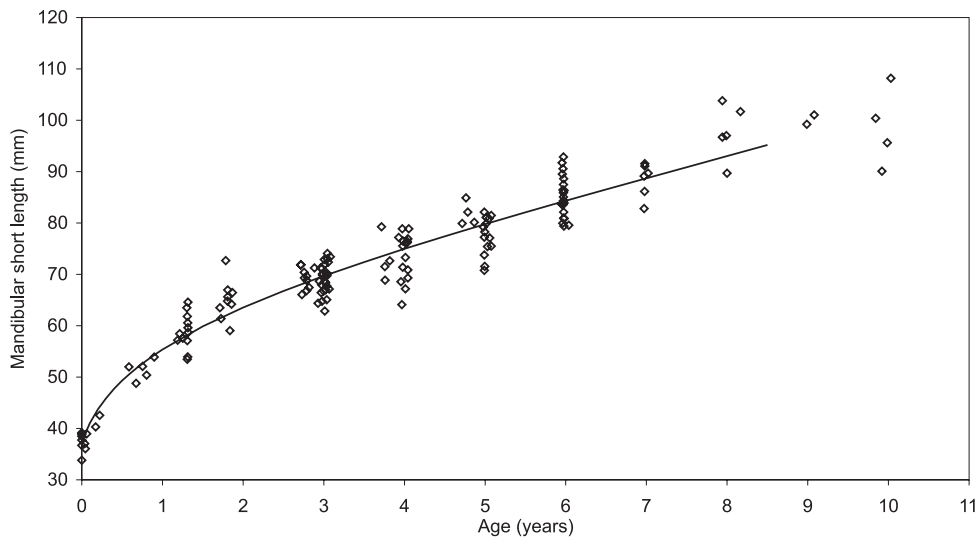


Fig. 2. Scatter plot of length-at-age data for mandibles from male northern fur seals collected between 1940 and 1953 ($n = 151$), with the corresponding von Bertalanffy growth curve.



there are numerous cyclic phenomena that act on interdecadal time scales that are likely to affect fur seal populations, prey availability, or both. In addition to the cycles specified by Trites and Bigg (1992) — 11-year cycle for sunspot activity (Waldmeier 1961) and 18.6-year cycle for lunar tidal node (Parker et al. 1995) — the Pacific Decadal Oscillation (PDO) might also be expected to affect prey availability in the North Pacific/Bering Sea (Ebbesmeyer et al. 1991; Francis and Hare 1994; Mantua et al. 1997). Finally, climatic forcing mechanisms that lack a clear cyclicality, such as the Aleutian Low pressure system, may also exert a direct influence on primary productivity in the North Pacific/Bering Sea (Trenberth and Hurrell 1994) and thus, indirectly, the availability of prey to fur seals.

Sunspot-activity cycles (Waldmeier 1961) appear to not play a role in this particular analysis, as both popmin and popmax span a complete cycle (Fig. 4a). The potential effects of variation in the lunar tidal node (Parker et al. 1995)

are less clear; samples representing popmin were collected during a period of low tidal heights, while samples representing popmax were collected during a transition from high to low tidal heights (Fig. 4b). With regard to the PDO, Mantua et al. (1997) identify only one major regime shift in the 20th century, in 1977, with minor regime shifts possibly indicated in 1925 and 1947. However, based on their yearly average PDO index (a unitless measure defined as the principal component of North Pacific monthly sea surface temperature variability), both time periods sampled here experienced primarily negative index values (Fig. 4c).

Another valuable index of climatic variability in the North Pacific that spans the 20th century is Trenberth and Hurrell's (1994) North Pacific Index. The North Pacific Index is the area-weighted sea-level pressure over the North Pacific (30–65°N, 160–140°W) averaged over the months November–March. Periods of relatively low sea-level pressure correspond to intensification of the Aleutian Low pressure system. In-

Fig. 3. Scatter plot of length-at-age data and the corresponding von Bertalanffy growth curves for male northern fur seals collected during popmin, 1911–1920 (—△—) and popmax, 1940–1953 (—◇—).

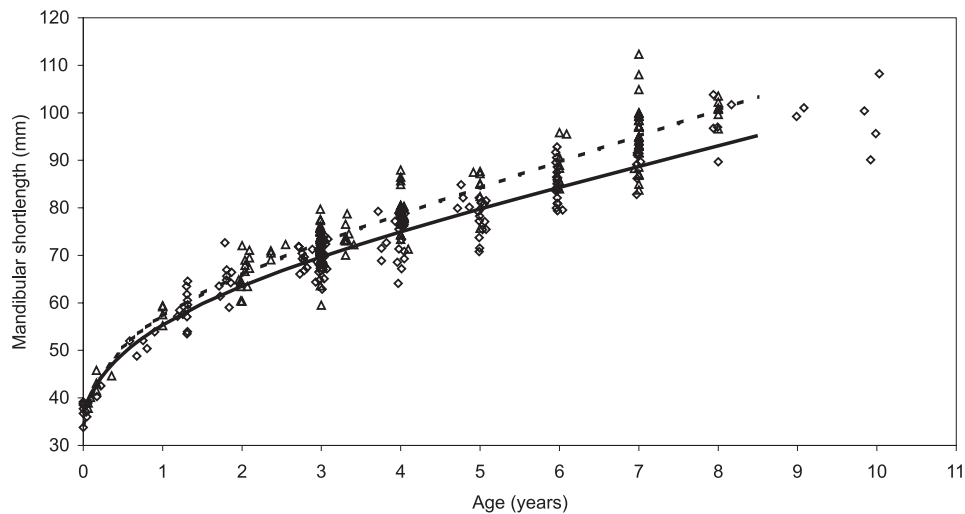


Table 3. Parameter estimates and summary statistics for von Bertalanffy growth curves generated using eq. 2 for popmin (1911–1920) and popmax (1940–1953).

	Parameter	Estimate	Asymptotic SE	Lower CI	Upper CI
Popmin ($R^2 = 0.912$, $n = 156$)	y_1	34.339	5.880	22.721	45.956
	y_2	100.610	0.982	98.670	102.551
	a	-0.283	0.122	-0.524	-0.041
	b	5.697	1.332	3.065	8.329
Popmax ($R^2 = 0.935$, $n = 151$)	y_1	36.682	1.401	33.914	39.450
	y_2	93.040	0.668	91.719	94.361
	a	-0.210	0.064	-0.336	-0.084
	b	5.472	0.751	3.988	6.956

Note: Starting values of 0.0 and 8.0 were used for T_1 and T_2 , respectively. CI, 95% confidence limits.

tense Aleutian Lows are, in turn, associated with increased upwelling and marine productivity (Trenberth and Hurrell 1994). With the exception of the winters of 1941–1942 and 1945, both popmin and popmax occurred during periods of weak Aleutian Lows (Fig. 4d). Importantly, the popmax sample is dominated by the 1940 and 1941 cohorts sampled at a variety of ages (Table 2). Because the intensity of the Aleutian Low pressure system scales inversely with marine productivity, much of the popmax sample should have experienced enhanced prey availability.

In summary, then, it appears that animals collected during both popmin and popmax experienced broadly similar climatic conditions characterized by negative PDO index values and periods of weak Aleutian Low pressure systems. The exception to this generality is the winters of 1941–1942 and 1945, which were relatively intense winters associated with increased upwelling and marine productivity. In spite of the differences in these key years, animals collected during popmax were smaller than animals collected during popmin.

Discussion

The challenge to any evaluation of variability in growth rates of fur seals is to identify (i) the relevant mechanism(s) behind variability in prey abundance and (or) distribution and (ii) a climatic data series with sufficient scope of detail

and coverage to make such an evaluation possible. Unfortunately, the specific effects that any given climatic perturbation may have on prey availability on either a local or a regional scale are largely conjectural, owing to a paucity of data from the early 20th century (Benson and Trites 2002; Sinclair and Stabeno 2002). Compounding this problem, fur seals travel thousands of miles annually along their migration route and consume over 60 different species of fish, squid, and krill (Kajimura 1984; Sinclair et al. 1994), whose overall contribution to the diet varies by region and year. The ability of fur seals to switch prey species, both temporally and spatially, has probably acted to buffer their populations to any but the most dramatic of shifts in oceanic productivity, making it difficult to predict whether shifts in productivity in the North Pacific, the eastern Bering Sea, or both would be significant. Furthermore, even if appropriate climatic data series were available, the mammalian communities of the North Pacific / eastern Bering Sea have undergone dramatic changes in abundance and composition over the past 200 years as a result of commercial harvests of pinnipeds (Busch 1985; Etnier 2002) and cetaceans (Trites et al. 1999; Springer et al. 2003), complicating analysis even further.

As the discussion above has made clear, there are a number of factors other than population level that could affect prey availability to fur seals and, by extension, the growth

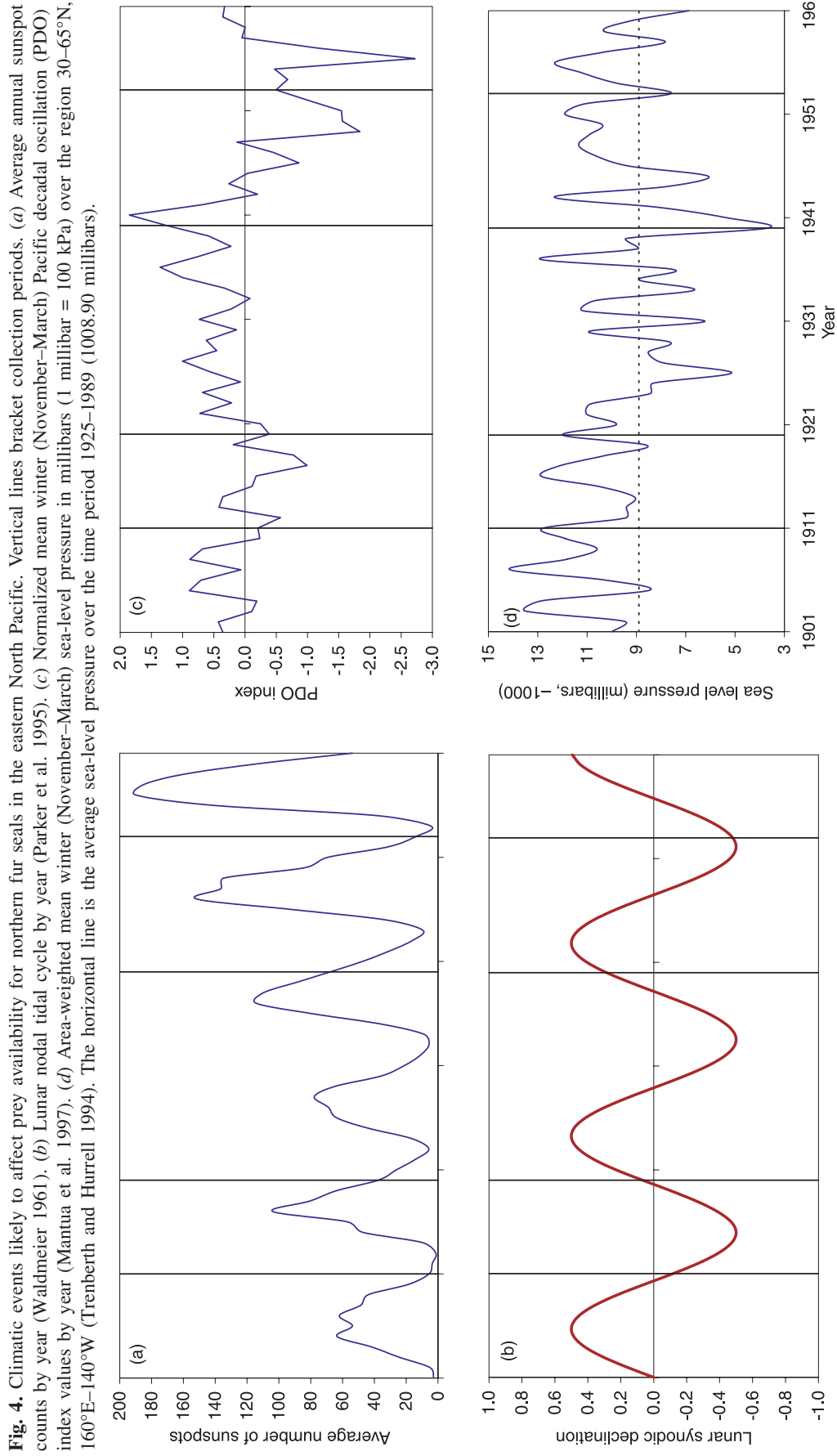


Fig. 4. Climatic events likely to affect prey availability for northern fur seals in the eastern North Pacific. Vertical lines bracket collection periods. (a) Average annual sunspot counts by year (Waldmeier 1961). (b) Lunar nodal tidal cycle by year (Parker et al. 1995). (c) Normalized mean winter (November–March) Pacific decadal oscillation (PDO) index values by year (Mantua et al. 1997). (d) Area-weighted mean winter (November–March) sea-level pressure in millibars (1 millibar = 100 kPa) over the region 30–65°N, 160°E–140°W (Trenberth and Hurrell 1994). The horizontal line is the average sea-level pressure over the time period 1925–1989 (1008.90 millibars).

rates of fur seals. However, the fact that multiple studies have reached the same conclusion, that growth is density-dependent, based on dramatically different samples deriving from a wide range of temporal periods, suggests that the burden of proof should shift: have prey populations in the North Pacific/eastern Bering Sea fluctuated during the 20th century to the extent that fur seal populations have been significantly affected? Mass-balance models suggest that although the Bering Sea is relatively resistant to perturbations, reductions in prey abundance can quickly reduce marine mammal populations (Trites et al. 1999). Until this has been tested empirically (e.g., through stable-isotope analysis of archived skeletal materials; see Burton and Koch 1999), the evidence suggests, on balance, that fur seal growth rates are driven by fluctuations in population levels rather than by fluctuations in their prey base.

Although far from definitive, the results presented here provide additional support for the hypothesis that growth rates of northern fur seals are density-dependent. The failure to find a solution for y_{∞} most likely relates to the sample of known-age individuals available from each time period. Nevertheless, the results indicate that individual fur seals grew to a larger overall size during popmin than during popmax: exactly the sort of difference expected under models of density-dependent growth.

This finding has significant implications for management of the current fur seal population. One of the possible explanations for the stabilization of the population at ~40% of the historic high is that there was a change in the carrying capacity (K) of the North Pacific / Bering Sea in the 1980s and 1990s (Sinclair et al. 1994). There is currently no explanation for the decline since 1998, but Fowler and Siniff (1992) suggested that pup survival rates in the 1980s might indicate a reduction of K by about 13%. Although a number of casual factors have been implicated, two of the most prominent are the major PDO of 1977 (Ebbesmeyer et al. 1991; Francis and Hare 1994; Mantua et al. 1997) and the continued development of the commercial groundfish industry (Trites and Bigg 1992; Bakkala 1993). The demonstration that fur seals are density-dependent in their growth rates provides a means to test this hypothesis. If the fur seal population has adjusted to a lower K , individual growth rates should be at a minimum. They should therefore be comparable to growth rates during the time period 1940–1955. In contrast, if the fur seal population is still well below K and something other than per capita prey availability is causing the population decline, growth rates should be at a maximum, comparable to growth rates during the time period 1910–1920.

Although adequate samples do not currently exist to test this hypothesis using VB growth curves based on mandibular measurements, the added support for the hypothesis that growth rates are density-dependent suggests that it may not matter what index of growth rate is measured. As long as comparable data (such as body size) can be generated for the time periods of interest, the current status of the fur seal population relative to K could, at least in theory, be evaluated (Fowler and Siniff 1992). Because a small-scale subsistence harvest of subadult male fur seals is still being conducted in the Pribilof Islands (Angliss and Lodge 2004), data of this nature should be easily obtainable.

In conclusion, the approach used here of analyzing archived skeletal material to evaluate density-dependent growth in fur seals has two distinct implications. The first, and most obvious, is that the results provide additional support for the hypothesis that individual growth rates of fur seals are density-dependent, and that variability in population levels can result in significant differences in growth rates. This does not deny the importance of other factors such as indirect competition with commercial fishing or climatic variability. Indeed, because the fur seal population is declining from an already depleted level (United States Code 1972; Angliss and Lodge 2004), an evaluation of the relative roles of commercial fishing and climate in maintaining the current population structure should now be possible.

The second implication of the results presented here is that it is possible to relate growth rates directly to population levels using measurements from skeletal material. This opens up the possibility of obtaining long-term data on relative population levels from palaeontological or archaeological samples. Because samples of this nature routinely span hundreds or thousands of years, the added time depth provided by these sources of data would make them a powerful tool for evaluating long-term trends in the population history of this species (Etnier 2002).

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