

Chapter 3: Evidence of density-dependent growth in northern fur seals (*Callorhinus ursinus*) based on measurements of archived skeletal specimens

Between the early 1950s and the 1970s, the Pribilof Islands, Alaska, population of northern fur seals (*Callorhinus ursinus*) declined approximately 60% (Sinclair *et al.* 1994; York 1990; York and Kozloff 1987) and has subsequently stabilized at a population level considered to be “depleted” under the Marine Mammal Protection Act (MMPA 1972; Sinclair and Robson 1999). Current management interests are aimed at understanding the various mechanisms that may have caused this decline. One of the mechanisms that has received considerable attention is density-dependent regulation of vital rates such as mortality, survival, and growth (Fowler 1990). The research presented here expands on previous efforts to understand variability in individual growth rate as a function of population levels through the analysis of archived skeletal material collected 1910-1955. If the reaction of fur seal growth to variability in population levels can be accurately modeled, biologists will have a valuable tool for evaluating the current population status and predicting future population trends.

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 1991; Baker and Fowler 1990; Fowler 1990; Trites and Bigg 1992). However, each of these studies utilizes different data (Table 3.1), 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 note-worthy time periods of fur seal population history in the 20th century (Figure 3.1): the period 1910-1920, when the fur seal population was at its historic low of between 200,000 and 300,000 individuals (Lander 1980; York 1987a) and the period 1940-1955, when the fur seal population had stabilized at its historic high of around 1.5 million (York 1987a). Hereafter I will refer to these two time periods as popmin and popmax, respectively. Importantly, both of these time periods pre-date the development of the extensive groundfish fishery in the North Pacific/Bering Sea (Trites and Bigg 1992, 1996). Thus, any variability in growth rates during in these two time periods should be related primarily to variability in the abundance of fur seals rather than fisheries-induced variability in the abundance of prey items (assuming no major oceanographic changes occurred over this time period: see discussion below). If variability in growth rates of northern fur seals is controlled primarily by population levels, individuals collected during popmin are expected to grow faster and/or to larger overall size than individuals collected during popmax.

Previous studies

Numerous researchers have attempted to document density dependent growth in northern fur seals. In spite of the wide variety of datasets 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 dates covered by the present study. However, Scheffer's analysis used mean measurements of

length, weight, skull length, and skull width for discrete age classes (summarized in Table 3.1) and then compared means between time periods. This approach limited Scheffer to comparisons between four discrete age classes (3-6 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 (1984, 1990) research on density-dependent growth in fur seals utilized a substantially different dataset than Scheffer to evaluate the same process. During the 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 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 levels 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. Trites and Bigg 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 fur seal population, the effects of the two variables may be confounded for samples collected after 1970 (Trites and Bigg 1992:135). 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 commercial fishing, samples should pre-date the 1960s. This marks the beginnings of the pollock (*Theragra chalcogramma*) fishery in the Bering Sea (Trites and Bigg 1992), which is a major component of the diet of fur seals (Kajimura 1984; Sinclair *et al.* 1994). Likewise, an index of size is needed that has low measurement error and that has a minimum of 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. Analysis of 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 mandible measurements from archived skeletal specimens that in most cases were collected specifically for age-determination studies (Osgood *et al.* 1915; Scheffer *et al.* 1984), with 156 mandibles from the time period 1910-1923 (popmin) and 161 mandibles from the time period 1940-1955 (popmax). The distribution of samples within each of the two time periods is shown in Figures 3.2a and 3.2b. As with all of the studies outlined above, this analysis will utilize cross-sectional, rather than longitudinal data, to estimate 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 1950c; Scheffer and Wilke 1953). Consequently, bone measurements from known-age specimens provide an index of the variability in 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), reducing the amount of background noise anticipated in the dataset. 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). Finally, and most importantly, the specimens utilized for this study were collected during the historic population low- and high-points. As such,

the data utilized here hold the promise of showing the maximum expected differences in growth patterns of any time period in the 20th century.

These time periods are delineated primarily by the collection years of known-age specimens and 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 (Trites 1992a; York and Hartley 1981).

For the purposes of this study, age has been calculated in fractions of years. As in Chapter 2, I have used the long-term average day of birth (7 July; Gentry 1998) to define zero age. I also assume that collection date is synonymous with the date of death of the individual. Given the remarkably synchronous birthing behavior of fur seals, 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 one or two months in error. However, a few individuals utilized in this study were aged via examination of the upper canine (following Scheffer 1950b). Thus, the age calculations are potentially in error by one year or more (Anas 1970). Error rates in age determination are assumed to be similar for both 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 Fowler UltraCal II 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 non-linear parameter estimation in SPSS (Norusis 1997). Although VB growth curves are most often found in the fisheries literature (Cerrato 1990; Fabens 1965; Kimura 1980; Schnute 1981), their general applicability to length-at-age data make them ideally suited for analyses of this type (c.f. Kingsley 1979; Leberg *et al.* 1989; McLaren 1993; Moscarella *et al.* 2001; 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

(Equation 3.1)
$$Y(t) = y_{\infty} [1 - e^{-g(t-t_0)}]^p$$

where $Y(t)$ represents size at age t , y_{∞} = the theoretical limiting size or asymptote, g represents the rate at which size approaches the asymptote, t_0 = 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 non-linear 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 (1981:1130), that which is most appropriate here is:

$$\text{(Equation 3.2)} \quad Y(t) = \left[y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-T_1)}}{1 - e^{-a(T_2-T_1)}} \right]^{1/b} .$$

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. The parameters a and b are equivalent to g and $1/p$, respectively, from Equation 3.1. That leaves y_1 and y_2 , the estimated average size at ages T_1 and T_2 . In addition to providing stable parameter estimates more reliably than Equation 3.1, Equation 3.2 eliminates the need to choose one of the several possible growth functions to describe a dataset (Knight 1968; Ricker 1979; Schnute 1981). Furthermore, the parameters estimated for Equation 3.2 can be used to calculate y_8 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 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

The age distribution of the samples has two important consequences for this analysis. The first is that the comparison of growth curves is only possible between 0.0 and 8.0 years of age (e.g., T_1 and T_2). Although this age range encompasses the majority of male fur seal growth, growth continues at a decreasing rate until the 10th year or so (Scheffer 1950b, 1950c; Scheffer and Wilke 1953). Individuals older than this were collected during these time periods. However, they have been identified only as “adult” or “>10 years,” and have been omitted from this analysis. The second consequence of the age distribution is that because the entire period of growth is not covered by the samples, no solution for asymptotic size (y_8) exists for either cohort (Schnute 1981).

Keeping these limitations in mind, Figures 3.3a and 3.3b plot MSL against age for each of the two time periods separately with the corresponding VB growth curves. In spite of the fact that no solution for y_8 can be calculated, examination of Figure 3.4 makes it apparent that the growth curves for the two time periods differ in the manner predicted under the hypothesis of density dependent growth: individuals sampled during popmin grew more quickly and/or to apparently larger size than during popmax. Summary statistics of the non-linear parameter estimates are listed in Table 3.2. The two terms describing the shape of the growth curves (a and b) are statistically identical in each cohort. However, the estimate of y_2 (e.g., size at age $T_2 = 8.0$) is significantly higher for popmin than for popmax.

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, there are numerous cyclic phenomena that act on inter-decadal time scales that are likely to affect fur seal populations, prey availability, or both. In addition to the cycles specified by Trites and Bigg (sunspot activity = 11 year cycle [Waldmeier 1961]; lunar tidal node = 18.6 year cycle [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; Niebauer and Day 1989).

The possibility that popmin and popmax experienced different climatic regimes is evaluated in Figure 3.5. Cycles in sunspot activity (Waldmeier 1961) appear to not play a role in this particular analysis as both popmin and popmax span a complete cycle (Figure 3.5, top). The potential effects of variation in the lunar tidal node (Parker *et al.* 1995) are less clear: samples representing popmin were collected during a transition from low to high tidal heights, while samples representing popmax were collected during the opposite transition (Figure 3.5, middle). Finally, Mantua *et al.* (1997) identify only one major regime shift (PDO) in the 20th century at 1977, with minor regime shifts possibly indicated in 1925 and 1947. However, based on their yearly average PDO index (Figure 3.5, bottom), both time periods sampled here experienced primarily negative index values.

Discussion

Despite the relatively small sample sizes used in this analysis, the results provide additional support for the hypothesis that growth rates of northern fur seals are density dependent and suggests that, at least for the time periods studied here, fluctuations in population levels of the fur seals drive this relationship rather than fluctuations in their prey base. The failure to find a solution for y_8 most likely relates to the sample of known-age individuals available for each sample. Nevertheless, the results indicate that fur seals grew to 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 has been a change in the carrying capacity (K) of the North Pacific/Bering Sea (Sinclair *et al.* 1994). Although a number of 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; Niebauer and Day 1989) and the continued development of the commercial groundfish industry (Bakkala 1989; Trites and Bigg 1992). 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. As such, they should be comparable to growth rates during the period 1940-1955. In contrast, if the fur seal population is still well below K, growth rates should be at a maximum, comparable to growth rates during the period 1910-1923.

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 of density-dependent growth rates suggests that it may not matter specifically how 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.

Implications for age estimates of unknown samples using growth curves:

In addition to the implications of these results for evaluating population levels relative to K, the significant variability in growth rates within a single population of fur seals over a relatively short time span has major implications for my proposal to use VB growth curves to estimate age-at-death for unknown samples. Depending on the relationship between the composition of the reference sample and the composition of the unknown sample, age of unknown samples may be systematically under-estimated, accurate, or systematically over-estimated (Table 3.3).

To evaluate the degree to which the relationship between the composition of the reference sample and the composition of unknown samples effects the accuracy of age estimates for the unknown samples, the VB growth curve generated for the full series of male mandibles ($n = 403$; see Chapter 2) will be used to back-calculate age-at-death for both popmin and popmax. Because the full reference sample spans the entire 20th century, including both popmin and popmax, the VB growth curve generated from the full sample can be considered to represent the long-term average growth rate for fur seal mandibles. Indeed, as Figure 3.6 shows, the VB growth curve for the full reference

sample is intermediate between the VB growth curves for popmin and popmax throughout most of the developmental sequence. The only portion of the developmental sequence for which the full reference growth curve is not contained between popmin and popmax is for ages younger than about one year. In this portion of the developmental sequence, the overall growth curve falls below both of the other two curves. This is likely due to the relatively small number of animals younger than one year sampled in popmin (25) or popmax (26) compared to the full reference (100 total; 49 exclusive of popmin and popmax, 18 of which are from San Miguel Island, California).

I will evaluate the accuracy of the back-calculations in two ways. The first regresses the age estimate based on MSL against true age. If the age estimate based on MSL is accurate, the slope of the regression will be statistically equivalent to 1.0. Over-estimates of age will lead to a slope greater than 1.0, while under-estimates of age will lead to a slope less than 1.0. The second way in which I will evaluate the accuracy of the back-calculations will be to examine the distribution of errors in age estimation (relative to true age). Although this is simply a different way of representing the same information contained within the regression analysis, it allows for easy visual evaluation of any patterning to the distribution of errors (Hartwig and Dearing 1979; Neter *et al.* 1996).

When age-at-death is back-calculated for mandibles deriving from popmin and popmax based on MSL, the results generally follow the predictions of the middle row of Table 3.3. Specifically, the regression line describing the relationship between true age and age estimated from MSL for popmin (Figure 3.7a) has a slope significantly higher than 1.0 ($p < 0.05$), regardless of whether the intercept is estimated from the data or

forced through the origin (see Table 3.4 for regression statistics). This indicates that MSL over-estimates age for popmin. Viewed another way, Figure 3.7b shows that the majority of the errors fall below the line $y = 0$, with an average over-estimation of 0.410 years.

The opposite pattern is observed for the back-calculated ages for popmax (Figures 3.8a and 3.8b). The slope of the regression line describing the relationship between true age and age estimated from MSL is 0.9263, which is significantly smaller than 1.0 ($p < 0.05$; see Figure 3.8a and Table 3.4). This is also demonstrated by the plot of errors in age estimation (Figure 3.8b), the majority of which fall above the line $y = 0$, with an average under-estimation of 0.298 years.

One of the patterns apparent in Figures 3.7a and 3.8a is that the distribution of errors is not uniform across age classes. For instance, in the back-calculations of age for popmax, most of the errors are for individuals aged 3-5 years. In contrast, most of the errors in the back calculations of age for popmin are between 4-8 years. In both cases, the magnitude of error increases with age, with relatively small errors in age determination up to one year of age followed by substantial errors throughout the rest of the developmental sequence. Furthermore, the distribution of errors for animals younger than one year generally follows the expectations of Figure 3.6, with both cohorts slightly over-estimated. Animals younger than one year were over-estimated an average of 0.124 months for popmax ($n = 26$, standard deviation = 0.942), and an average of 0.511 months for popmin ($n = 28$, standard deviation = 1.196; see Figures 3.9a, 3.9b).

Conclusions

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 my results provide additional support for the hypothesis that individual growth rates of fur seals are density dependent, and that variability in population levels alone 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 currently stable, but characterized as depleted (MMPA 1972; Sinclair and Robson 1999), it should now be possible to evaluate the relative roles of commercial fishing and climate in maintaining the current population structure.

The second implication of my results is that it is possible to relate growth rate directly to population levels using measurements from skeletal material. This opens up the possibility of obtaining long-term data on relative population levels from paleontological or archaeological samples. I will return to this issue in Chapter 6, using a series of 230 male mandibles from the Ozette archaeological site in western Washington.

Finally, the back-calculation of age based on MSL shows a clear patterning to the distribution of errors. Even in the best-case scenario where the reference growth curve represents the long-term average growth rates, errors in age-estimation can be substantial, and tend to increase with age. For animals older than about three, the direction of the bias will depend on the relative population level. For animals younger than one year, calibration of MSL against the VB growth curves based on the full reference sample

slightly over-estimate age, with the magnitude of the over-estimation dependent on the relative population level.