

Chapter 2: Modeling bone growth in northern fur seals (*Callorhinus ursinus*)

There is a brief but very useful and informative biography of an individual contained within the skeleton, if you know how to read it.

---Clyde Snow (1997)

The purpose of this chapter is to develop a means of estimating age at death of northern fur seals (*Callorhinus ursinus*) on the basis of growth patterns of selected skeletal elements (see Howell 1929; Lyman 1991b; Lyon 1937; Repenning *et al.* 1971; Snodgrass and Gifford-Gonzales n.d. for characters useful in identifying *C. ursinus* skeletal remains). As noted in the introduction, the impetus for this research is based largely on the observation that the archaeological distribution of fur seals in the eastern North Pacific matches very poorly with the distribution expected based on nearly 200 years of scientific study (Burton 2000; Burton and Koch 1999; Burton *et al.* 2001, 2002; Fiscus 1978; Gustafson 1968; Lander 1979; Lyman 1988, 1989, 1991b, 1995; Scheffer 1958; Scheffer *et al.* 1984). Thus, any tests of the “historic effects” hypothesis outlined in Chapter 1 require an evaluation of the degree to which the prehistoric distribution of fur seals differs from the historically documented distribution. This will be accomplished, in part, through the generation of demographic profiles of fur seal remains recovered from archaeological sites in the eastern North Pacific (see Chapter 5) using the skeletal measurements detailed here.

The use of mortality profiles in archaeofaunal studies

Archaeologists have recognized for quite some time that determinations of age at death of animal remains recovered from archaeological sites can provide a wealth of information on subsistence practices, including seasonality (reviewed in Monks 1981;

see also Todd 1991; Woodborne *et al.* 1995), basic procurement strategies (Friesen *et al.* 1998; Frison 1978; Klein 1982; Klein *et al.* 1981; McCartney 1995; McCartney and Savelle 1993; Savelle and McCartney 1991), and long-term impacts of hunting pressure (Klein and Cruz-Uribe 1983; Klein *et al.* 1999; Koike and Ohtaishi 1985, 1987; Smith 1985; Woodborne 1996). In addition to information on human behavior, demographic profiles of archaeofaunas can provide tests of hypotheses concerning the stability of biogeographic patterns when taxa have age-specific and/or sex-specific patterns of behavior (Bryden 1972; Etnier 2002; Gustafson 1968; Lyman 1988, 1989, 1991b, 1995; Lyon 1937; Parkington 1972; Woodborne *et al.* 1995; Woodborne 1996). With specific reference to fur seals, the marked differences in migration patterns of adult males on the one hand, and adult females and sub-adults of both sexes on the other (see Chapter 1), provide a basis for interpreting the biogeographic significance of archaeological samples of fur seal skeletal material—if these age classes can be reliably identified.

The basis for studies of this sort is firmly grounded in theoretical population biology (Beverton and Holt 1957; Caughley 1966, 1977) and empirical studies of modern populations (Fiscus 1978; Lander 1979; Stiner 1991). Detailed mathematical models have been developed to describe the demographic structure expected in unmanaged populations (i.e., under the influence of little or no human hunting: see Figure 2.1a), populations harvested at varying levels of sustainable yield, and the changes in demographic structure expected when populations are harvested at a rate higher than can be replaced with annual recruitment (i.e., higher than the maximum sustainable yield, or MSY: see Figure 2.1b).

The first challenge to archaeologists is to calculate the demographic structure of the archaeofaunal assemblage. This requires characteristics observable in the skeleton that correlate with age (or size: see Bryden 1972; Burton *et al.* 2001) that can also be reliably measured on archaeological material. Once this is accomplished, the demographic, or harvest, profile generated from what is termed the death assemblage (Lyman 1987, 1991a; Stiner 1991) can be used to draw inferences about the various aspects of subsistence practices discussed above.

The use of mortality profiles in archaeological analyses of fur seal hunting

Annular structures in otariid teeth have long been used for accurate and precise age determinations in zoological research (Oosthuizen 1997; Payne 1978; Scheffer 1950b). This is without question the most reliable means of determining age at death of fur seals (Anas 1970). Consequently, little effort has been expended to characterize growth patterns of the remainder of the skeleton (but see Scheffer 1950c; Scheffer and Wilke 1953). Nevertheless, fur seal canines are not commonly used in archaeological analyses because teeth are relatively rare compared with post-cranial remains in archaeological contexts. Furthermore, detailed examination of the annuli requires thin-sectioning of the teeth—an inherently destructive form of analysis.

As an alternative to the destructive analyses of teeth, a common approach is to assign post-cranial skeletal elements to broad age categories based on degree of development and the fusion state of epiphyses of long bones (Calvert 1980; Huelsbeck 1983; Lyman 1988, 1991b; Porcasi *et al.* 2000; Yesner 1977, 1988). The most frequently used age categories are: adult (epiphyses fully fused); sub-adult (element

approaching full size but epiphyses not fused); juvenile (element relatively small, epiphyses not fused); and, pup/newborn/fetus (element extremely small and poorly ossified; see Calvert 1980; Huelsbeck 1983; Lyman 1988, 1991b; Lyon 1937; Porcasi *et al.* 2000; Smith 1985; Yesner 1977, 1988).

Although patterns of epiphyseal fusion have been used extensively to characterize broad age categories in different species of fur seals (Calvert 1980; Huelsbeck 1983; Lyman 1991b; Lyon 1937; Smith 1985; Woodborne *et al.* 1995; Woodborne 1996; Yesner 1977, 1988), this approach to characterizing the age distributions of fur seals is problematic for two main reasons. The first is that age classes based on state of epiphyseal fusion bear little relationship to behaviorally meaningful age classes (e.g., immature vs. reproductively mature); the second is that identification of the youngest age classes relies heavily on subjective criteria.

The first problem relates to the fact that patterns of epiphyseal fusion vary considerably between sexes, among individuals, and even among different elements within an individual. Males, for instance, reach puberty in the fourth or fifth year (Gentry 1998), begin to reproduce as early as seven or eight years old (Figure 2.2), and continue to grow well beyond the age of 10 (Scheffer and Wilke 1953). In contrast, females reach sexual maturity at age two, typically reach sociological maturity (i.e., begin to breed) in their fourth year, and continue to grow slowly until about age 10 (Gentry 1998; Scheffer and Wilke 1953; York 1983, 1987b; York and Scheffer 1997).

The dramatic dimorphism in growth patterns of males and females makes it difficult to interpret age categories based on epiphyseal fusion, particularly when it is

realized that most post-cranial elements lack characters with which to distinguish sex until they are nearly fully developed. However, much more problematic is the fact that fur seals continue to grow after they have reached sociological maturity. Although a large proportion of this growth can be expected to be accomplished through the addition of muscle and blubber (Scheffer and Wilke 1953; Trites and Bigg 1996), preliminary ontogenetic studies indicate that bone growth and epiphyseal fusion may post-date the attainment of sociological maturity in pinnipeds (Versaggi 1981). If this were true for fur seals, then age categories based on patterns of epiphyseal fusion would bear little or no relationship to the behaviorally meaningful age categories of interest.

The second reason that categorizing post-cranial fur seal remains on the basis of epiphyseal fusion is problematic relates to the difficulty of reliably distinguishing between late-term fetuses, newborn pups, and weaned pups. Accurate identification of these age classes is critical to understanding seasonal resource use. But more importantly, identifying the presence of newborn pups is the only way to document the exploitation of rookeries (Lyman 1988, 1989, 1991b, 1995). Without this ability there is little hope of understanding variability in fur seal migration and breeding distributions during the Holocene. Although it is theoretically possible to distinguish these youngest of age classes via direct comparison with known-age reference material, skeletons of this age are relatively rare in research collections (e.g., Calvert 1980). Until recently, the most convincing evidence for low latitude fur seal rookeries had been presented by Lyman (1991b:170), and this was based on comparison of archaeological specimens with only four known-age specimens (two aged two years and two aged three years, sex not

indicated). More recently, Burton *et al.* (2001) estimate body length based on regressions between mandible length and body size developed from 34 known-age fur seal specimens ranging in age from pups to adults. The estimates of body length were then converted to approximate age categories (Burton *et al.* 2001). Although this represents an improvement on Lyman's approach, there is nevertheless room for progress in how age-at-death is estimated for skeletal remains of fur seals.

Characterizing general bone growth

The remainder of this chapter details characteristics of bone growth in northern fur seals based on observations and measurements of known-age skeletons curated in museum collections throughout the country (Appendix A). However, some general considerations of bone growth need to be presented before moving to the observations and measurements of the reference skeletons. Measurements of cranial elements, which develop as dermal bones, have been presented elsewhere by Scheffer and Wilke (1953). Therefore, this discussion will involve primarily the development of endochondral bones, or those that are initially formed as cartilage. The two exceptions are the mandible, which in mammals develops as dermal bone (Romer 1963), and the baculum, which is characterized as a heterotopic bone, or one that develops through the ossification of connective tissue rather than cartilage (Romer 1963). An extensive series of mandibular measurements will be presented below. Measurement data for the baculum have been presented elsewhere (Scheffer 1950c), but additional unpublished measurements have been made available (Scheffer *pers. com.*) and will be presented in full in the appendix, along with a series of new measurements for this element.

Endochondral bones of fur seals grow in the same manner as the bones of other mammalian taxa. That is, cartilaginous precursors of the element are gradually ossified through the deposition of bone minerals by osteoblasts (Romer 1963). Many elements such as the carpals and tarsals consist of a single center of ossification. Consequently, continued growth is theoretically possible as long as cartilage is present. In taxa that approximate indeterminate growth, such as fur seals (Costa *et al.* 1988; Trites and Bigg 1996), elements of this type are expected to approximate logarithmic growth throughout their lifetime (Figure 2.3a).

In contrast to the carpals and tarsals, long bones develop from multiple centers of ossification (Romer 1963). Although also expected to approximate logarithmic growth, long bones will differ from the previous example in two important respects. The first is that growth can only continue as long as the cartilaginous metaphyseal plate persists between the epiphyses and the long bone shaft, or diaphysis. Thus, once the epiphysis has fused to the diaphysis, growth in that area stops (assuming growth due to bone remodeling after epiphyseal fusion is insignificant). The second difference is that, rather than the monotonic growth curve illustrated by Figure 2.3a, long bone length is expected to demonstrate a step-function with the fusion of each epiphysis (Figure 2.3b). The number and size of steps will vary by element and by measurement within an element. For instance, metacarpals develop from two centers of ossification, consisting of a diaphysis and a single epiphysis (Carlson 1967; Greulich and Pyle 1959), and would only demonstrate a single step function in length. In contrast, measurements will obviously not be affected by epiphyseal fusion if the landmarks do not include the

relevant metaphysis (e.g., dimensions of the proximal end of an element would not be affected by fusion of the distal epiphysis).

Characterizing bone growth in northern fur seals

This study utilizes measurements of skeletal elements from specimens of northern fur seals for which age is either known or could be estimated. Due to varying completeness of the reference skeletons, sample size varies considerably from one element to the next. The most complete data exist for the mandible, with approximately 400 each of males and females (Table 2.1, Appendices A, B), and reasonably even coverage across age classes (Figures 2.4a, 2.4b). In contrast, the post-cranial elements consist of a maximum of 44 females and 51 males (smaller sample sizes for some elements), with relatively poor distribution across age classes (Appendices A, B, Figures 2.5a, 2.5b).

The large sample of known-age specimens utilized for measurements of the mandible and baculum is the result of decades of detailed research on the northern fur seal populations in the Pribilof Islands, Alaska. In most cases these specimens were collected specifically for age-determination studies (Osgood *et al.* 1915; Scheffer 1950a; Scheffer *et al.* 1984). The methodology involved marking fur seal pups by tagging and/or branding when they were only a few months old. For instance, 5228 pups were marked in 1912. Likewise, 5000 pups were marked in 1940, 10,000 in 1941, and 20,000 per year between 1947 and 1949 (Scheffer 1950a). In the years following pup marking, samples of marked individuals (of known age) were killed in the commercial and subsistence harvests of males, and their crania and baculae archived in museums and

research collections (Scheffer *et al.* 1984). In addition, large numbers of females were killed in pelagic research cruises between 1958-1974. Crania of known-age females were also archived in museums and research collections (Lander 1980; Wilke 1951).

Complete skeletons are much less common in research collections, and even fewer of those are of known age. In cases where age was not known, or could not be determined by examination of growth annuli in the canine teeth (Scheffer 1950b), I estimated age using growth curves developed from the mandibular measurements (Figure 2.6; see Table 2.2 for measurement definitions). For the purposes of this study age has been calculated in fractions of years, with an age of zero corresponding to date of birth (but see Trites 1991, Trites and Larkin 1989 who use date of implantation to define zero age). Fur seals have a narrow interval during which pups are born, with virtually all of the births falling within a few weeks of the mean birthing date (Bartholomew and Hoel 1953; Peterson 1968; Trites 1992b). Although the mean birthing date is earlier in the San Miguel population (24 June; DeLong 1982) than in the Pribilof population (7 July; Gentry 1998), locality information for the skeletal specimens was used to determine the appropriate mean birthing date. Specimens for which locality information was not recorded, or was ambiguous regarding population origin, age was rounded to the nearest whole month or whole year, depending on the specificity of collection information. I further 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, most of the calculated ages are not likely to be more than one or two months in error. A few individuals utilized in this study were aged via examination of the upper canine. For these individuals, the age calculations are potentially in error by one year or more (Anas 1970). Finally, the precision in age estimates based on mandibular measurements will vary by age, with larger error terms for older individuals.

Evaluating systematic bias in reference samples:

In addition to concern regarding the precision of age estimates based on skeletal measurements, this study assumes that the reference samples analyzed here provide an unbiased (e.g., accurate) means of estimating age-at-death for unknown samples—regardless of the temporal and/or spatial origin of those samples. Three factors are likely to influence the validity of this assumption: variability in the cause of death of the individuals in the reference samples (particularly young-of-the-year, or YOYs), latitudinal variability in growth patterns, and density dependent variability in growth patterns.

The first of the potentially biasing factors is that many of the individuals in the reference sample were recovered as stranded YOYs. Given that malnutrition is a common cause of death in stranding cases (TMMC 2001), these individuals may be considerably smaller and underdeveloped relative to healthy individuals of the same cohort. Balancing this potential bias, many of the pup skeletons from the Pribilof Islands population were either sacrificed specifically for ontogenetic studies (Scheffer and Wilke 1953) or were natural mortalities collected opportunistically from the rookeries. Because a high proportion of pup deaths on rookeries is the result of trauma (Keyes 1965), healthy

individuals from the Pribilof Islands population should be well-represented in the reference sample. In point of fact, the overwhelming majority of reference samples derive from the Alaskan population (Table 2.4, Appendices A, C). Thus, the inclusion of stranding victims in the reference sample is not likely to significantly bias the characterization of the first year of growth.

The preponderance of Alaskan animals in the reference sample, however, may potentially bias the growth curves in another way. There is some indication that body size in geographically distinct populations of pinnipeds varies with latitude (McLaren 1993). Although this hypothesis has not been tested for fur seals in the eastern North Pacific, anecdotal evidence suggests that the fur seals from the Alaska population are larger than the fur seals from the California population (Sharon Melin *pers. com.*). If body size in fur seals varies with latitude, growth curves based primarily on a single population may lead to systematic errors in age estimation for samples deriving from any other population. The geographic distribution of the reference specimens analyzed here is such that, if fur seals exhibit latitudinal differences in body size, the strongest bias would be expected in age estimates based on the mandible (Table 2.4, Appendices A, C). This is due to the fact that 95% of male mandibles, and 79% of female mandibles derive from the Alaska population. The distribution of post-cranial skeletons is more equitable for males, with 71% of male skeletons from Alaska. The distribution of female skeletons is the same as for female mandibles (79%). The potential effects of this source of bias will be evaluated at length in Chapters 3 and 6.

The third factor that may bias the accuracy of age estimates based on calibration of skeletal measurements with growth curves is density dependent variability in growth rates. Although the extent to which the growth rates of fur seals varies with population density is still debated (Trites and Bigg 1992), the Alaska population of fur seals has exhibited significant variability in individual growth rate throughout the 20th century (Baker 1991; Baker and Fowler 1990; Fowler 1990; Scheffer 1955). As with the potential effects of latitudinal differences in body size, the potential bias introduced by density dependent variability in growth rates will be evaluated in Chapters 3 and 6.

Measurements of northern fur seal elements

Despite the fact that several archaeologists have utilized skeletal measurements of pinniped elements for age-determinations (Burton 2000; Burton *et al.* 2001; Lyman 1991b; Parkington 1972; Smith 1985; Stanford 1976; Woodborne 1996) there has been little effort to standardize the measurements made on post-cranial elements. I am aware of only one other systematic study of post-cranial pinniped skeletons for the eastern North Pacific. That unpublished study (Snodgrass and Gifford-Gonzales n.d.) is designed, in large part, to develop osteological and metric characters to distinguish skeletal material from each of the six species of pinnipeds extant in the eastern North Pacific, and is based primarily on fully fused, adult skeletons. Considering the fact that juveniles and sub-adults often represent a significant proportion of the pinniped bones recovered in archaeological sites, measurements need to be designed that can easily accommodate changes in morphology associated with ontogenetic development and

epiphyseal fusion. Finally, measurements of skeletal elements are only useful if the relevant landmarks used to define the measurement preserve archaeologically.

In an effort to make the fur seal skeletal measurements as broadly applicable as possible, several measurements were made on each element (Tables 2.1, 2.2). In general, total length of each element was measured, along with various measurements of the proximal and distal ends, where appropriate. When epiphyses were unfused, measurements were taken with the epiphysis removed. Measurements were taken with a Fowler UltraCal II digital calipers and recorded the nearest 0.01 mm.

As will become evident from the growth data for skeletal measurements presented here and in the appendix, there is a remarkable degree of redundancy in the measurements for any given element, with virtually every measurement correlating strongly with age over several years of ontogenetic development. This is advantageous in that it allows age estimations to be calculated on a wide range of elements and portions of elements recovered from archaeological sites.

In general, the measurements described here correspond closely with those developed independently by Snodgrass and Gifford-Gonzales (n.d.) for fully fused elements. In addition to the various measurements detailed here, state of epiphyseal fusion was noted for each element. Specimens that were clearly pathological or structurally damaged were not measured.

The patterns of bone growth in the mandible, the humerus, and the calcaneus will be discussed in detail here. While each of these elements has broadly similar growth characteristics, the specific growth pattern of each element, as well as the applicability to

archaeological samples varies considerably. Details for all other measured elements can be found in the appendix.

The data presented in the remainder of this chapter will provide a general framework for estimating age-at-death of fur seal skeletal material. The measurement data for fur seal skeletal elements will be presented in a number of different ways. First, males and females will be plotted separately, with an appropriate mathematical characterization of the growth patterns (e.g., linear or non-linear). Second, the timing of epiphyseal fusion will be described insofar as can be determined from the available data. Finally, plots and growth equations will be provided for both sexes combined for the cases where it is not possible to distinguish sex based on characteristics of size and degree of development of the skeletal element.

The relationship between size and age will be characterized by a von Bertalanffy (VB) growth curve (von Bertalanffy 1938, 1960) 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 (cf. Kingsley 1979, McLaren 1993; Winship *et al.* 2001).

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

(Equation 2.1)
$$Y(t) = y_{\infty}[1 - e^{-g(t-t_0)}]^p$$

where $Y(t)$ represents size at age t , y_8 = 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 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:

$$\text{(Equation 2.2)} \quad Y(t) = \left[y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-T_1)}}{1 - e^{-a(T_2-T_1)}} \right]^{1/b} .$$

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 2.3. 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 2.3, Equation 2.4 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 2.4 can be used to calculate y_8 and t_0 if they exist (which will not always be the case; see Schnute 1981).

The Mandible

In many respects the mandible provides more life history information than any other element of the fur seal skeleton. In addition to a close correlation between mandible size and age (Smith 1985; Woodborne 1996), sex determinations are easily accomplished if a portion of the canine alveolus is present (Etnier 2002; Huber 1994; Lowry and Folk 1990; Scheffer and Kraus 1964). Finally, if the canine tooth is present, growth lines evident in longitudinal sections of teeth can provide an independent estimate of age (Scheffer 1950b), a measure of growth rate of the individual (Antonelis *et al.* 1982), and data on the length and frequency of nursing events during the first few months of life (Baker 1991).

The mandibular measurement that is most commonly used in archaeological contexts is termed short length (Burton 2000; Burton *et al.* 2001; Etnier 2002; Parkington 1972; Snodgrass and Gifford-Gonzales n.d.; Woodborne *et al.* 1995; Woodborne 1996), 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 (see Figure 2.8, Table 2.2). As can be seen from Figure 2.9, mandibular short length (MSL) correlates quite closely with age. Indeed, of the six mandibular measurements presented here, MSL has the highest correlation coefficient (r^2) values for both males and females (Table 2.4). Nevertheless, despite lower r^2 values than MSL, each of the other mandibular measurements shows a strong positive relationship with age (Figures 2.10-2.14; Table 2.3).

One of the surprising characteristics of the growth curves for the mandible is that, although the sexual dimorphism of the species (Scheffer 1958; Scheffer and Wilke 1953) is clearly evident in the overall relationships between mandible size and age, there is substantial overlap in the measurements for males and females. This characteristic of the growth curves underscores the difficulty of distinguishing males from females when the canine and/or canine alveolus is absent.

Because of the broad overlap of mandibular measurements, regression statistics are also presented for both sexes combined (Table 2.3). Examination of the plots in Figures 2.9-2.14 makes it clear that for each measurement there is a maximum dimension females are not likely to exceed (cf. Bryden 1972). For instance, the greatest MSL for any female mandible is 82.39 mm, with good representation of measurements from older individuals in the asymptotic region of the growth curve. Thus, mandibles with MSL greater than 84.00 mm can be confidently identified as male. Because of this, only those mandibles with MSL less than 84.00 mm are included in the non-linear regression of MSL against age for both sexes combined. The other mandibular measurements are treated in similar fashion, with the specific size cut-off listed in parentheses next to the specific measurement listed in Table 2.3.

The humerus

Growth in long bones such as the humerus is more complicated to model than growth of the mandible. The same general pattern of approximately logarithmic growth is expected, with the end result reflecting the sexually dimorphic size differences (Figure 2.6). However, as discussed above, the ontogeny of long bones includes the parallel

development of between 2 and 5 centers of ossification that ultimately fuse into a single bone (Carlson 1967; Greulich and Pyle 1959; Romer 1963). As I have discussed, any measurement that includes a metaphyseal region as a landmark will be expected to demonstrate a step function in the growth curve following the fusion of the associated epiphysis (Figure 2.3). To further complicate matters, the timing of the fusion of epiphyses is a function of both sex (Greulich and Pyle 1959; Romer 1963; Versaggi 1981) and age (Scheffer and Wilke 1953). The degree to which the timing of fusion varies with latitude or with population density (cf. Fowler 1990; Scheffer 1955) is presently unknown. Nevertheless, inasmuch as documentation of the timing of these events will be helpful in determining age at death, the accuracy of age-at-death estimations of samples of unknown age relies heavily on the ability to distinguish males from females.

The largest sample of known-age post-cranial measurements presented here has been compiled for males (Table 2.1; see Figure 2.7, Table 2.2 for measurement definitions). However, due to the distribution of ages represented, very little can be determined regarding the timing of epiphyseal fusion. For instance, despite the fact that 51 individuals have been measured, only two of these (aged 10 and 14) have fully fused humeri (Figure 2.15). The distal epiphysis of the humerus is fused in two other specimens, aged approximately 8-9 years. The remaining 45 specimens lack any epiphyseal fusion of the humerus. Because of the small sample of individuals older than seven years, it is difficult to determine the variability in the timing of the fusion of the distal and proximal epiphyses. Nevertheless, the data presented here support the

argument that pinnipeds continue to grow substantially after reaching both reproductive and sociological maturity (cf. Versaggi 1981).

The critical time periods of the development of female humeri have better coverage than for males, with 13 fully fused individuals, four with only the distal epiphysis fused, and 29 lacking any fused epiphyses (Figure 2.16). From this sample, it appears that the distal epiphysis fuses in females between three and five years of age and the proximal epiphysis fuses between four and six years of age. As with the patterns suggested by humerus growth in male fur seals, female fur seals continue to grow well after attaining reproductive and sociological maturity.

In terms of metric characterizations of humerus growth in fur seals, some interesting patterns emerge. Measurements of total length for both sexes (Figures 2.15, 2.16) follow the generalized pattern discussed above of approximately logarithmic growth punctuated by step functions coincident with the fusion of each epiphysis (Figure 2.3b). Curvilinear growth is most clearly represented prior to fusion of the distal epiphysis. However, due to the small sample size, little can be determined concerning growth of the humerus in the period between fusion of the distal and proximal epiphyses. Finally, and contrary to the model presented in Figure 2.3b, humerus growth stops once the proximal epiphysis has fused, as indicated by the non-significant linear relationship between total length and age in the fully fused humeri of females (Figure 2.16; $p = 0.279$). Likewise, distal width in both males and females (Figures 2.17, 2.18) does not increase significantly with age after fusion of the distal epiphysis (males, $p = 0.499$; females, $p = 0.118$).

When the patterns of epiphyseal fusion of the humerus are coupled with sex-specific measurements, these data can be used to distinguish males from females in many cases. As with the mandible, there are linear dimensions that female humeri are not likely to exceed (Bryden 1972). For instance, the greatest total length that an unfused female humerus can reasonably be expected to attain is around 90.00 mm (Figure 2.16). In contrast, unfused male humeri reach a maximum total length of about 141.00 mm (Figure 2.15). Thus, any unfused fur seal humerus greater than 90.00 mm is identifiable as a male. In similar fashion, sex can be determined for humeri with fused epiphyses based on reference to the plots in Figures 2.15-2.18 and the data in Appendix C.

Finally, another similarity between the growth patterns of the humerus and the mandible is that there is a high degree of overlap in measurements among juveniles (Figure 2.6). As with the mandible, it is difficult or impossible to distinguish male humeri from female humeri when they are in this age range. Following the protocol established for the mandible, VB growth curve parameter estimates for the humerus are presented for males, females, and both sexes combined, with the appropriate size cut-off for the identification of males listed in parentheses for the combined data in Table 2.3. The main difference between the data presented for the mandible and the data presented for the humerus is that only completely unfused humeri have been utilized for the parameter estimates. The presence of a fused epiphysis establishes the sex and likely age range of the individual, but can provide little additional information on age at death.

The calcaneus

As discussed above, most of the tarsals and carpals develop as endochondral bones from a single center of ossification (Greulich and Pyle 1959; Romer 1963). Thus, the development of these elements would be expected to approximate logarithmic growth without any step functions during development. The exception to this general pattern is the calcaneus, which is unique among podials in that it develops from two centers of ossification: the main body of the element and a small epiphysis at the *tuber calcus*. However, because of the small size of this epiphysis, epiphyseal fusion is not expected to significantly affect measurements that include the *tuber calcus* as a landmark (Figure 2.19; Table 2.2).

Examination of the plots of calcaneus length (Figure 2.20) shows that this is only partially the case. The three fused male calcanei, for instance, have an average total length of 65.00 mm, while the asymptotic maximum size of the unfused male calcanei approaches 56.50 mm: a difference of 8.5 mm. In contrast, the larger sample of fully fused female calcanei ($n = 7$; see Figure 2.20), has an average size of 46.8 mm, but the asymptotic maximum size of the unfused female calcanei approaches 45.0 mm: a difference of just under 2.0 mm. As with different aspects of humerus growth, the linear relationship between age and the length of fully fused calcanei in females is not significant ($p = 0.053$), again because growth of this element stops with epiphyseal fusion.

Unlike the fusion patterns in the humerus, the fusion of the epiphysis at the *tuber calcus* spans a relatively large age range. Female calcanei can apparently fuse as early as

five years or so, but a nine year old female in the sample had an unfused calcaneus. The much smaller sample of males of an appropriate age suggests that the calcaneus fuses in males somewhere between 8-10 years of age.

Discussion and Conclusions

The growth patterns presented in this chapter for three different skeletal elements, each with slightly different ontogenetic properties, all serve to illustrate several general patterns of bone growth in northern fur seals (generalized in Figure 2.21). These patterns are an approximately logarithmic growth curve, an inability to distinguish sex in juvenile skeletal elements, a clear dimorphism in size after about 4-6 years of age, and the continuation of growth after attainment of reproductive and sociological maturity. The same general patterns appear to hold regardless of the element, or specific measurements within that element (the measurements presented in the appendix reinforce this conclusion).

If the patterns of skeletal growth documented here can be assumed to be representative of fur seal growth in the eastern North Pacific, these data provide a valuable tool for estimating age at death for unknown samples. As discussed above, the traditional method of assigning fur seal skeletal material to broad age categories based on state of epiphyseal fusion can be misleading. Not only are the age categories extremely coarse, but they also do not serve to distinguish biologically meaningful age classes such as newborns, migrating YOYs, or individuals that have reached reproductive and/or sociological maturity. Although direct comparison of unknown specimens with known age specimens can be instructive (Lyman 1991b), synoptic comparative collections are

rarely adequate to provide estimates of age at death for the full range of ages represented in archaeological assemblages (Calvert 1980).

The data presented here and in the appendix provide an alternative approach for determining age at death for a wide variety of skeletal elements and portions of elements. This approach is based on the relationship between skeletal dimensions and age developed from a large sample of reference specimens whose age was known or could be estimated. These data include published and unpublished measurements of specimens from seven museums located throughout the United States. As such, they represent the most comprehensive compilation of skeletal measurements of northern fur seal skeletons published to date.

Nevertheless, there are still significant gaps in the representation of age classes for post-cranial measurements of both sexes (Figure 2.5). Furthermore, as discussed above, the degree to which the timing of fusion varies with latitude or with population density (cf. Fowler 1990; Scheffer 1955) is presently unknown. Based on the work of Fowler (1990) and Scheffer (1955), in addition to data presented in Chapters 3 and 6, this variability is expected to be substantial. When these gaps are filled with measurements and observations of additional specimens whose ages span the relevant developmental periods, collected from a range of population densities and latitudes, the results presented here concerning the timing and variability of bone growth in fur seals may well change.