Neoglacial Sea Ice and Life History Flexibility in Ringed and Fur Seals

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Two interesting life history questions about North Pacific pinnipeds beg for zooarchaeological input. One is the observation that the ringed seal, *Phoca hispida*, an Arctic species that also inhabits the Bering Sea, appears to have two morphologically distinct ecotypes: (1) a large, territorial form that gives birth and breeds on the immobile, shorefast ice (aka "fast ice") that forms along terrestrial shorelines; and (2) a smaller, early maturing form that lives and breeds offshore, within the mobile Arctic pack ice (aka "sea ice"). The existence of two distinctly sized ringed seal ecotypes, initially brought to the attention of biologists by Inuit hunters (e.g., Brendan Kelly, University of Alaska SE, Juneau, pers. comm.), has since been confirmed by scientific research directed specifically at this topic (Fedoseev 1975; Finley et al. 1983) and corroborated by other studies on general ringed seal biology (Born et al. 2004; Davis et al. 2008; Ferguson et al. 2000; Ferguson 2006; Wiig et al.

1999). At issue, however, is whether offshore-breeding ringed seals constitute a significant portion of the global population or a very minor one.

Certainly, distinct ecological morphotypes that differ in size (an example of so-called resource polymorphism) are well documented in a number of other vertebrate species. Mammalian examples include Antarctic killer whales (*Orcinas orca*; Pitman and Ensor 2003; Pitman 2004; Pitman et al. 2007), minke whales (*Balaenoptera acutorostrata*; Arnold et al. 1987; Reeves et al. 2002, Best 1985), bottlenosed dolphins (*Tursiops truncata*; Charleton et al. 2006; Tezanos-Pinto et al. 2008; Morin et al. 2006), African elephants (*Loxodonta africana*; Debruyne et al. 2003; Debruyne 2005), and bison (*Bison bison*; Geist 1990, 1998; Wilson 1996). Numerous other examples are known among birds, reptiles, and amphibians (Skúlason and Smith 1995; Smith and Skúlason 1996) and may include one or more differences in morphology,

behavior, life history characteristics, and color. Such ecological plasticity has been shown to be critical to evolutionary survival, especially in unstable environments (Keeley et al. 2007; Leimar et al. 2006; Smith and Skúlason 1996). Therefore, skeletal size variation within a population that is discernable from zooarchaeological remains, and which correlates to distinct ecological habitats, may be an indicator of important life history flexibility and ecological plasticity. If a significant portion of the global population of ringed seals lives and breeds exclusively in offshore pack ice, and is characterized by its small size, should we not expect noticeably small ringed seal remains to be strongly represented in zooarchaeological assemblages from sites occupied by maritime-adapted hunters who routinely exploited pack ice habitat throughout the Arctic?

Another phenomenon of interest is the evidence we now have from archaeological sites along the west coast of North America that northern fur seals (NFS), which currently migrate annually to breeding rookeries in the Bering Sea (Gentry 1998), formerly established rookeries as far south as California that were attended by nonmigratory animals (Crockford et al. 2002; Etnier 2002; Moss et al. 2006: Newsome et al. 2007). None of these satellite rookeries are older than about 4500 BP (all dates are radiocarbon years before present, uncalibrated, unless stated otherwise), and several appear to have survived into the late historic period (Crockford et al. 2002; Lyman 1988, 1989; Gifford-Gonzalez et al. 2005). While we have evidence that maternal nursing regimes were also different among nonmigratory fur seals (Burton et al. 2001; Newsome et al. 2007), no one has yet advanced a reason for such a major shift in life history strategy. Modern records confirm that this species is remarkably consistent in its habits and has been for more than a century: the peak date of birth on the Pribilof Islands has been virtually unchanged in over 100 years (Bigg 1990; Elliot 1887; Gentry 1998) and NFS are noted for their remarkable migratory drive and natal site fidelity (e.g., Baker et al. 1995; Baker 2007). What would

prompt a change to this apparently rigid life history pattern?

We propose that comprehensive analysis of prehistoric marine mammal remains from a site in the eastern Aleutians, occupied at the height of the Middle Holocene Neoglacial, may assist in answering the above questions about ringed seals and fur seals because both species inhabit the Bering Sea portion of the North Pacific (Figure 4.1) during critical periods of their life history. The Neoglacial was a period of cold climate that lasted from approximately 4700 to 2500 years ago in most regions (e.g., Calkin et al. 2001; Dyke and Savelle 2001; Mason and Barber 2003; Razjigaeva et al. 2004). Any associated increases in seasonal pack ice in the Bering Sea during that time would have affected all marine mammals utilizing the region, as pack ice conditions virtually define this ecosystem: the extent of seasonal pack ice each year is governed by wind moving ice south from the Arctic through the Bering Strait (Rigor and Wallace 2004). During most of the 20th century, the pack ice front reached its southern-most position sometime in April (about as far as the Pribilof Islands, rarely beyond) and receded quickly thereafter (Grebmeier et al. 2006; Overland and Stabeno 2004). In other words, the Pribilofs have always been in a strategically vulnerable position in relation to seasonal Bering Sea pack ice.

While most resident pinniped species in the Bering Sea utilize pack ice as a mobile platform for giving birth, mating, and moulting (so-called pagophilic, or ice-obligate, taxa), a few temperate species utilize ice-free terrestrial beaches in the southern region for such purposes. Pagophilic species include walrus (*Odobenus rosmarus*), bearded seal (*Erignathus barbatus*), ringed seal (*Phoca hispida*), spotted seal (*Phoca largha*), and ribbon seal (*Phoca faciata*), while temperate species include the northern fur seal (*Callorhinus ursinus*), Steller sea lion (*Eumatopias jubata*), and harbor seal (*Phoca vitulina*). For the purpose of this discussion, we assume that habitat types utilized by these species for giving birth and mating were not appreciably different during the Neoglacial than they are today.
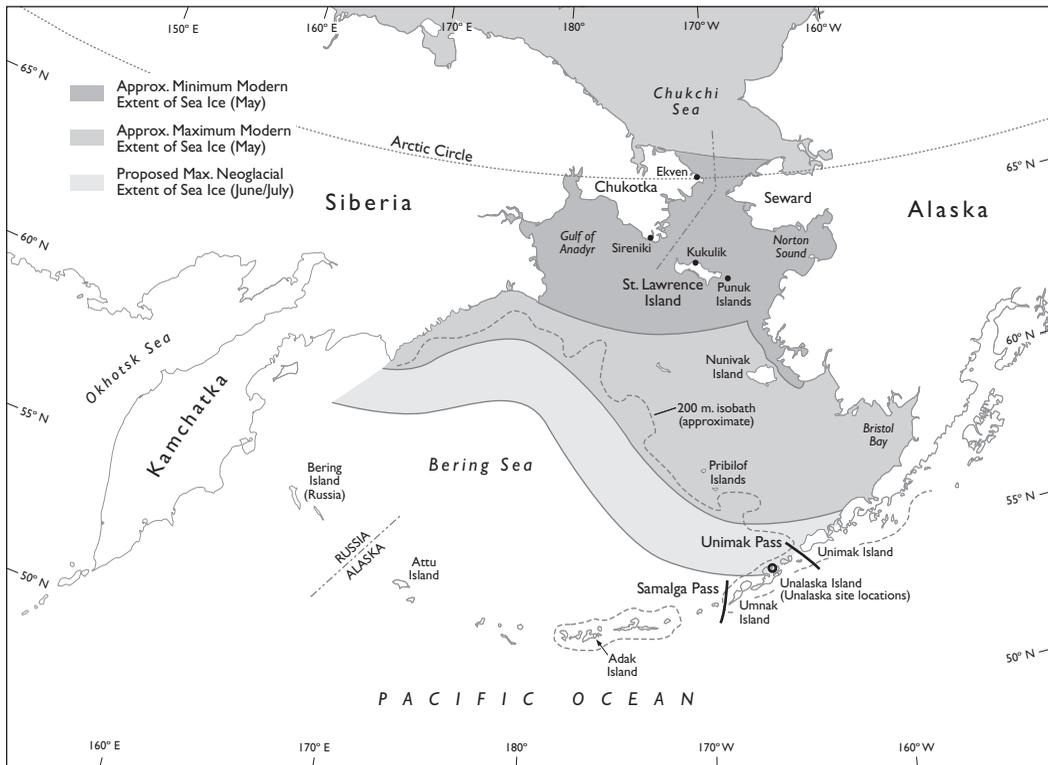
FIGURE 4.1. Modern minimum/maximum extent of spring pack ice (May) for the central and eastern Bering Sea (from http://www.beringclimate.noaa.gov/essays_mcnutt.html), with proposed maximum Neoglacial pack ice extent (June/July). Amaknak Bridge, UNL-050, is located on a small island off Unalaska, circled (adapted from Crockford and Frederick 2007).

Here we provide evidence that Neoglacial sea ice expansion (Figure 4.1) pushed Bering Sea populations of pack ice–breeding ringed and bearded seals south as far as the eastern Aleutians and kept them there until early summer, making these Arctic-adapted species easily accessible to ancient Aleut hunters. Extensive pack ice development would also have made the Pribilof Islands unsuitable as early summer pupping grounds for fur seals, forcing them to establish rookeries away from ice-covered waters and icy winds. These conclusions are based on a comprehensive analysis of skeletal remains recovered from an archaeological site off Unalaska Island in the eastern Aleutians (Figure 4.2) that was occupied at the height of the Neoglacial period, ca. 3500 to 2500 BP. Attention to taxonomic identity of postcranial phocid seal remains and estimation of ontogenic age for all taxa was instrumental in generating unique proxy evidence that

pack ice extent in the southern Bering Sea changed markedly during the Neoglacial (Crockford and Frederick 2007), which sheds significant new light on the origins of Thule culture (Crockford 2008) and on important aspects of ringed seal and fur seal life history.

AMAKNAK BRIDGE ZOOARCHAEOLOGY

REGIONAL SETTING

The eastern Aleutians have been occupied by people for at least 9000 years (Knecht and Davis, 2001). The Amaknak Bridge site (UNL50) is located on Amaknak Island in Unalaska Bay near the seaport of Dutch Harbor and the city of Unalaska (Figure 4.2), on an old marine terrace about 2 meters above present sea level. Archaeologists Rick Knecht, Museum of the Aleutians, and Rick Davis, Bryn Mawr College,
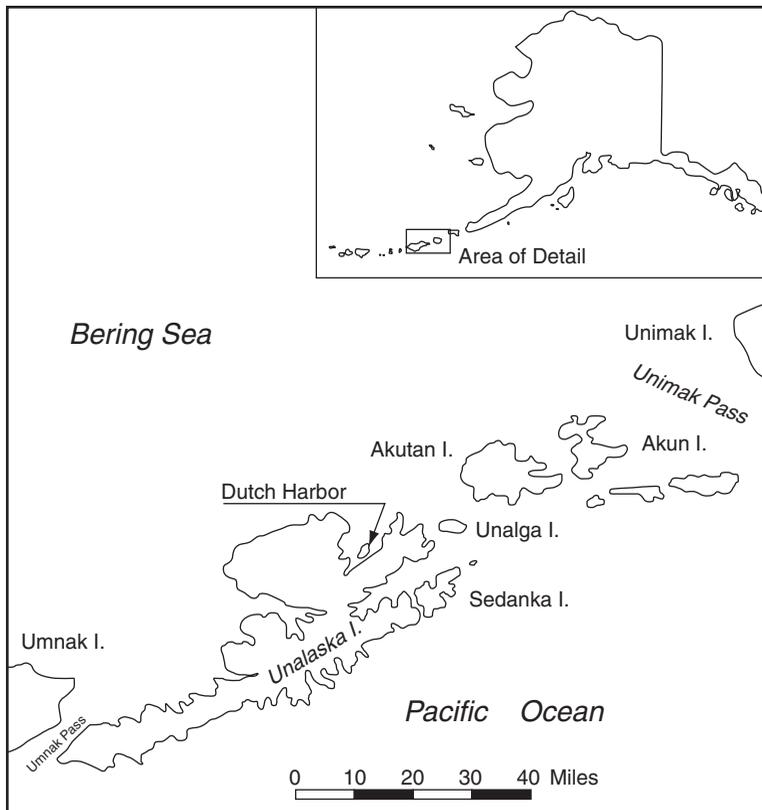
FIGURE 4.2. Location of the fishing port of Dutch Harbor on Unalaska Island, the general locale of the Amaknak Bridge site, near the modern city of Unalaska (from Knecht and Davis 2004).

conducted salvage excavations at the site over the summer of 2003 (Knecht and Davis 2004, 2008), exposing several semi-subterranean dwellings and associated shell middens containing well-preserved animal bone.

ZOOARCHAEOLOGICAL ANALYSIS METHODS

A representative subsample of the bird, fish, and mammal remains was analyzed, with a total of 42,359 specimens identified to family level or better (5947 of these are mammal). Basic quantification is by Number of Identified Specimens (NISP). Age-at-death for young juveniles (<1 yr) and sex determinations for pinnipeds were based on comparison to modern specimens of known age and sex (listed in Appendices 4.1 and 4.2), as well as published references (Etnier 2002, 2004; Storå 2000). This approach vastly

increases the amount of information discernable, even for phocid seals (e.g., Hodgetts 2005; Storå and Lõugas 2005). General age estimates for animals > 1 yr are based on relative size and epiphyseal fusion: unfused epiphyses and smaller than adult size are "juvenile," fused or partially fused epiphyses with suture lines evident, close or equal to adult size, are "subadult," while those with fused epiphyses and no suture lines evident are "adult."

Age-at-death determinations were crucial to our interpretation of this assemblage, especially for the two dominant species (NFS and ringed seal). We spent extra effort determining species identity for as much of the small phocid seal component of the sample as possible and for ringed seals, this also entailed an assessment of putative ecotypes. These topics are discussed in more detail below.

AGE-AT-DEATH DETERMINATION, NFS

Age of juvenile NFS remains was estimated using four comparative fur seal skeletons from animals with approximate known ages (see Appendix 4.2 for descriptions; see Crockford et al. 2002 for measurements of selected elements). These specimens compare favorably (estimated age vs. size) with measurements reported by Etnier (2002, 2004) for a much larger sample. We also had a subadult female (epiphyses unfused, ca. 2–3 years old) and a fully adult male (epiphyses fully fused, >8 years) available for comparison.

As an additional check against our subjective age estimation method, all measurable specimens of mandible, humerus, radius, ulna, femur, and tibia that had been judged subjectively to be young juvenile or younger (based on comparison to modern specimens of known age) were selected for comparison to the large sample of modern juvenile fur seal measurements reported by Etnier (2002, 2004). All Amaknak Bridge NFS that were assessed subjectively as either "young juvenile" (newly weaned, ca. 4–6 months) or "newborn" (unweaned, less than 4 months) fell within or below the range of measurements of modern animals estimated by Etnier to be between 1 and 10 months of age (Crockford et al. 2004), suggesting that the additional step of measuring archaeological bones did not increase the level of accuracy in age estimates. This is almost certainly due to the fact that few truly known aged animals exist in any collection (i.e., animals tagged the day of birth). As is true for most specimens of wild species, all NFS specimens are assigned the mean pupping date for the species as their "birth date" and age is then back-calculated from the date of death or date of collection.

AGE-AT-DEATH DETERMINATION, RINGED SEALS

As most of the prehistoric ringed seal remains from the Amaknak Bridge site were immature, we attempted to estimate an ontogenic age for as many specimens as possible. Jan Storå (2000) has provided valuable data on fusion times and sequences for postcranial elements of ringed seal, based on comparative specimens collected in the Baltic Sea. In total, he examined 97 complete skeletons of ringed seal and 29 incomplete ones. Unfortunately, only two specimens represent the critical newborn period (<2 months, "skeletal age 1") and only one represents the next developmental stage ("skeletal age 2"). As a consequence, the fusion dates he gives for the youngest ages are based on a very small sample and given the bias in collection of ringed seals discussed above, these almost certainly represent the large, shorefast ecotype. However, the data complement information gathered from comparative specimens of harbor seal in the University of Victoria collection and ringed seal material we examined from other institutions (see Appendix 4.1). Storå's study identifies several useful developmental events for estimating the age of young ringed seals, which we summarize below. He notes that the sequence of fusion is the same in all species, although the precise timing of individual fusion events may vary somewhat.

- Fusion of vertebral bodies to the arches begins at about 3 months of age and is complete by 6 to 8 months (Figure 4.3a, b). Fusion starts with the cervicals and is followed by the lumbars; the thoracics fuse last. A line of fusion between centrum and arch may be visible, especially in the thoracics, until early in the second year of life. Thus, completely unfused vertebral bodies and arches definitely represent animals less than 3 months of age.

- Fusion of the distal epiphysis of metacarpus I usually starts at 2 months of age.

- Fusion of the distal epiphysis of metatarsus I does not usually start until 3 months of age.

- Fusion of the acetabulum (pelvis) usually begins at about 3 months of age (Figure 4.3c).

- Fusion of the proximal epiphysis of the humerus (head to greater tubercle components) usually begins at about 4 months of age.
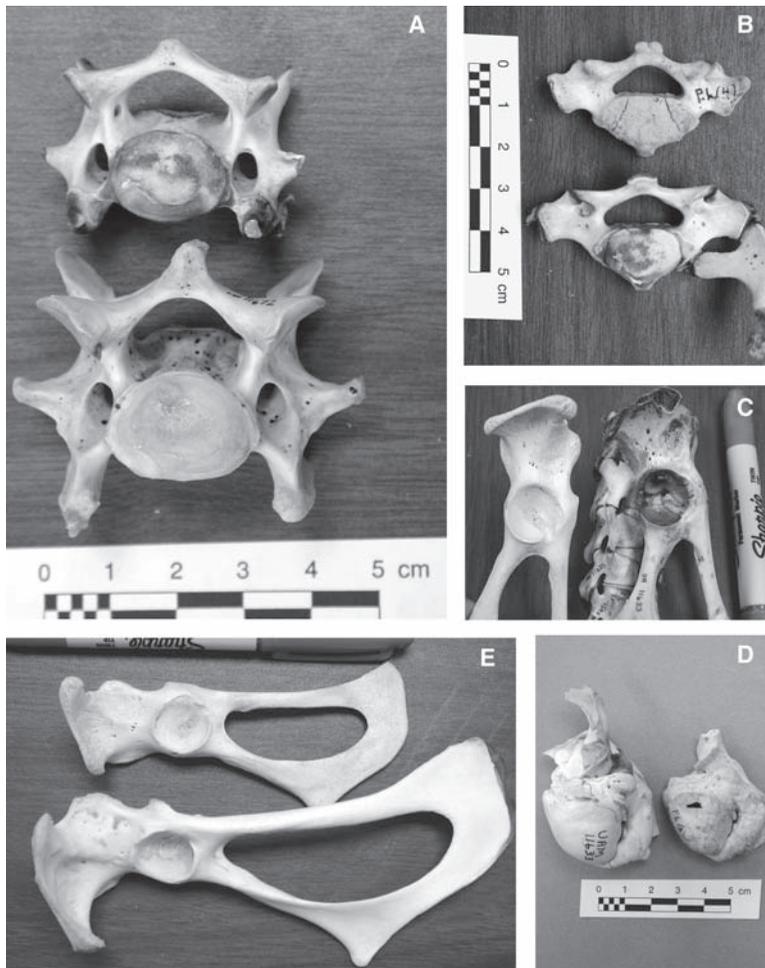
FIGURE 4.3. Ringed seals, ecotype size and development. (A) Top to bottom, cervical vertebrae (C6) of juvenile (shorefast ecotype), UAM 11633 (8–12 wks), vs. adult female (pack ice ecotype), UAM 11672. (B) Top to bottom, thoracic vertebrae (T1) of Amaknak Bridge juvenile (putative pack ice ecotype), AB 201438, vs. juvenile (shorefast ecotype), UAM 11633 (8–12 wks). (C) Left to right, innominates of Amaknak Bridge juvenile (putative pack ice ecotype), AB200133, vs. juvenile (shorefast ecotype), UAM 11633 (8–12 wks); see text for discussion. (D) Left to right, auditora bullae, juvenile (shorefast ecotype), UAM 11633 (8–12 wks), vs. Amaknak Bridge juvenile (putative pack ice ecotype), AB 200121. (E) Top to bottom, innominates of Amaknak Bridge juvenile (putative pack ice ecotype), AB200133, vs. adult female (pack ice ecotype), UAM 11672. See Appendix 4.1 for notes on modern specimens (UAM numbers).

- Fusion of the supraglenoid tubercle of the scapula does not usually begin until about 5 months of age.

TAXONOMY OF ARCTIC PHOCIDS

North Pacific phocids have distinct life history characteristics that may prove invaluable to the interpretation of a zooarchaeological assemblage, and thus unless a species identity can be determined for as much of the phocid component of a sample as possible, there may be a significant loss of valuable information. However, it has been customary for those working on North Atlantic seals, for which there is a relatively long history of analysis, to be very conservative regarding taxonomic identifications be-

cause of real and/or perceived difficulties in distinguishing among smaller species. This tradition extends back at least as far as Jeppe Møhl's work on prehistoric seal remains from Greenland over 30 years ago (Møhl 1979) and has been adopted by many eastern North American faunal analysts (e.g., Woollett et al. 2000). While certain identification problems certainly exist for phocid seal remains, as discussed below, we contend that limiting identification of phocid species to a few skeletal elements (e.g., auditory bullae, bony palate, maxillae, mandibles, and humeri only, as per Woollett et al. 2000) may result in an unnecessary reduction of sample size and, potentially, a significant loss of valuable information.

We believe that a more rational approach to small phocid bone identification is needed for North Pacific taxa. If humeri of small seals are judged to be diagnostic to species, there is no valid reason to expect that other postcranial elements will not be equally distinctive. For example, Møhl's (1979) analysis of material from Nugarsuk in northwest Greenland included ulnae as well as humeri (with illustrations of both, showing diagnostic features). We suggest that the question of whether a particular element from closely related species is diagnostic is often more a question of available time, effort, and access to adequate comparative material, rather than lack of distinctive taxonomic differences.

A good example of this phenomenon is provided by the closely related species pair of harbor seal and spotted seal, which are very similar in external appearance. Spotted seals are truly pagophilic: they give birth primarily on ice and are associated with pack ice for much of the year. They are found only in the North Pacific (mostly in the Bering Sea and Okhotsk Sea) and their distribution overlaps with that of harbor seals over a narrow zone in the south only, where hybridization is known to occur. Although a complete biological assessment, published decades ago, led Shaughnessy and Fay (1977) to conclude that the spotted seal is a distinct and separate species, the taxonomy was

not changed to reflect this until it was confirmed by mitochondrial DNA analysis (O'Corry-Crowe and Westlake 1997; Mizuno et al. 2003). As a consequence, the old taxonomy (which considers the spotted seal a subspecies of *P. vitulina*) predominates in pre-21st-century literature for virtually all biological and archaeological studies of the region.

Shaughnessy and Fay (1977) described cranial and mandibular features between these two species, including the shape of the auditory bullae, the glenoid fossa of the skull, and the alignment of the premolar teeth (which are straight in spotted seal and oblique in harbor seal, Figure 4.4a). Since traditional taxonomy seldom considers the postcranial skeleton, it is not surprising that only cranial and mandibular features are mentioned in Shaughnessy and Fay's comparison. However, our analysis suggests that differences in the shape of other skeletal elements also separate these two species, particularly the articular surfaces of all major limb elements (femur, tibia, radius, and ulna) (Figure 4.5). Although beyond the scope of this paper, a comprehensive comparison of the postcranial skeleton of these two species would definitely be useful.

In contrast, the bearded seal, the largest, most ancient, and most genetically distinct of the arctic phocid seals (Arnason et al. 2006), has very distinctively shaped skeletal elements that are virtually impossible to confuse with any other species, even for juvenile remains. The very large size of newborns, which are slightly longer than newborn walrus (Burns 1970; Reeves et al. 2002), make distinguishing even neonatal bearded seal remains rather straightforward. Similarly, in our opinion, virtually all ribbon seal skeletal elements are highly diagnostic for all age classes (Figure 4.5), including carpals and tarsals of young juveniles. The ribbon seal is another strictly North Pacific pagophilic species with a very distinctive pelage (Burns 1970; Reeves et al. 2002)—its uniquely banded hair coat seems to echo the degree of skeletal difference from other small seals in the
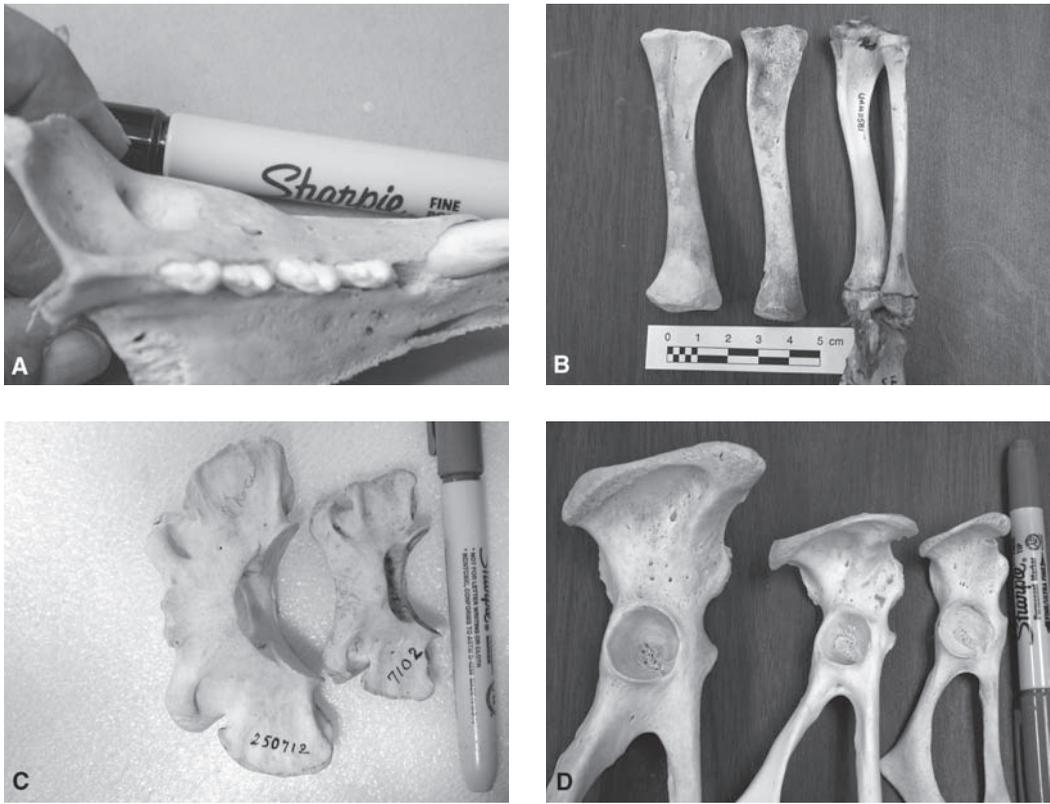
FIGURE 4.4. (A) Upper left maxillary tooth row of spotted seal, UAM 11675, showing the straight tooth alignment characteristic of this species (cf. diagonal alignment in the closely related harbor seal). (B) Species differences in shape for the tibia of some juvenile seals, left to right: spotted seal, UAM16605 (2–4 wks); Amaknak Bridge ringed seal, AB 200152; ringed seal, UAM 11581 (6–8 wks). (C) Species differences in shape and size for the cervical vertebra # 1 (atlas), left to right: adult harbor seal, NMNH 250712, vs. adult ringed seal, NMNH 7102. (D) Species differences in shape and size for the innominate: adult male spotted seal, UAM 11675; adult female ringed seal (pack ice ecotype), UAM 11672; Amaknak Bridge ringed seal, AB200133. See Appendix 4.1 for notes on modern specimens (UAM/NMNH numbers).

region. While the ribbon seal is genetically distinct from all other North Pacific seals (Arnason et al. 2006), it is quite closely related to the Atlantic harp seal (*Phoca groenlandicus*): together, ribbon and harp seals comprise the second-most-ancient lineage of Arctic phocids.

We also found ringed seal skeletal elements to be highly diagnostic in size and shape. These skeletal differences are almost certainly a reflection of their evolutionary antiquity: of all Arctic phoicids, only the bearded/hooded seal and ribbon/harp seal groups are older (Arnason et al. 2006; Harington 2008). While there is some size overlap between large ringed seals and small harbor or spotted seals, there are significant morphological shape differences in

most postcranial skeletal elements, irrespective of size or age (Figures 4.4 and 4.5).

RINGED SEAL ECOTYPES

All prehistoric remains of adult ringed seal we examined from the Amaknak Bridge site were significantly smaller than museum specimens available for comparison that had been collected from nearshore locations with shorefast ice, as were most juvenile remains of similar developmental stage (Figure 4.3). Ringed seals in the Bering Sea inhabit both pack ice (large sheets or chunks of sea ice that drift with the currents and wind) and shorefast ice (immobile ice attached to land, aka "fast ice"). While it is often stated that animals found in the pack ice

FIGURE 4.5. Top row, shape difference between adult ringed seal and other species in proximal femur shape, left to right: (A) harbor seal, UVic 86/85, vs. ringed seal, UAM 11672; (B) spotted seal, UAM 11675, vs. ringed seal, UAM 11672; (C) ribbon seal, UAM 11469, vs. ringed seal, UAM 11672. Middle row, shape difference between species of phocid seals (adult), distal tibia/fibula: (D) ringed seal, UAM 11672; (E) ribbon seal, UAM 11469; (F) spotted seal, UAM 11675; (G) harbor seal, UVic 86/85. Bottom row, shape difference between species of phocid seals (adult), L. humerus: (H) left to right, spotted seal, UAM 11675, harbor seal, UVic 86/85, ribbon seal, UAM 11469, ringed seal, UAM 11672. See Appendix 4.1 for notes on modern specimens (UAM/UVic numbers).

are groups of nonbreeding subadults that have been excluded from preferred territories in shorefast ice by older, dominant animals (Hammill and Smith 1991; Holst et al. 1999; Krafft et al. 2006, 2007; Laidre et al. 2008; Smith and Hammill 1981; Smith et al. 1991; Stirling and Øritsland 1995), it is has been clear for some time that the pack ice is not restricted to

immature animals. Evidence of ringed seal breeding in the pack ice comes from the Bering Sea (Burns 1970), Sea of Okhotsk, and Chukchi Sea (Fedoseev 1975), Davis Strait of the central Canadian Arctic (Finley et al. 1983), and the Barents Sea (Wiig et al. 1999).

Fedoseev (1975) concluded from his preliminary study in the North Pacific that pack

TABLE 4.1
Subset of measurements from adult male ringed seals (≥ 8 yr), fast ice vs. pack ice specimens
Body measurements in cm; cranial measurements in mm.

MEASUREMENT	N	FAST ICE MEAN (± SD)	N	PACK ICE MEAN (± SD)	P
Body length	5	133.5 ± 4,58	9	125.1 ± 3.89	** <0.01
Zygomatic width	4	112.3 ± 1.45	6	104.5 ± 3.21	** <0.01
Mastoid width	4	112.0 ± 1.98	7	106.1 ± 2.07	** <0.01
Width of occipital condyles	4	58.7 ± 1.35	8	56.2 ± 1.85	* <0.05
Length of tympanic bullae	5	38.9 ± 2.16	9	36.6 ± 1.57	* <0.05
Length of lower tooth row	5	50.5 ± 1.65	8	47.9 ± 1.21	** <0.01
Length of upper tooth row	5	57.2 ± 2.71	9	53.9 ± 1.29	** <0.01
Length of lower jaw	5	114.6 ± 3.56	8	107.6 ± 3.67	** <0.01

NOTE: From Finley et al. 1983, table 3. Specimens archived in the National Museum, Ottawa, catalogue numbers NMC 45419-45469. Highly significant values for *p* are marked **.

ice–breeding seals were smaller at maturity as well as at birth and that they matured faster than shorefast ice–breeding seals. Finley and colleagues provided morphometric evidence from Baffin Bay in support of Fedoseev's work, of which we present a subsample here (see Table 4.1): Baffin Bay pack ice seals were not only smaller but matured about a year earlier than shorefast-breeding seals. In conclusion, Finley et al. (1983:171) suggested that the age structure of the pack ice population they analyzed "approximates that of a normal breeding population."

Despite the evidence that two distinct morphotypes indeed exist—apparently the consequence of the population dividing itself among two distinct ecological habitats that are consistently available across the Arctic—ringed seals are characterized as giving birth invariably within shorefast ice habitats exclusively (e.g., Frost et al. 2004; Hammill and Smith 1991; Holst et al. 1999, 2001; Kingsley et al. 1985; Laidre et al. 2008; Lydersen and Gjertz 1986; Reeves et al. 2002; Smith and Hammill 1981; Smith et al. 1991; Stirling and Øritsland 1995). Where pack ice–breeding is acknowledged to occur, it is largely dismissed

as an insignificant phenomenon (e.g., Burns 1970; Krafft et al. 2007; Nowak 2003). However, given that offshore pack ice throughout the Arctic remains virtually unsurveyed for all life forms, including polar bears and ringed seals (e.g., Aars et al. 2006), such a conclusion must be considered premature.

Some biologists have concluded that a substantial population of ringed seals must inhabit the offshore Arctic pack ice, based in part on estimates of the number of seals required to support known populations of polar bears, their primary predator (e.g., Stirling and Øritsland 1995; Wiig et al. 1999; Derocher et al. 2002; Stirling 2002). Finley et al. (1983:171), based on a survey of Baffin Bay in the central Canadian Arctic, concluded that "the pack ice supports a much larger population of seals than does the bordering area of fast ice" and that these animals inhabit ice that lies well offshore. This offshore habitat is probably beyond the reach of biologists' survey aircraft, which seldom manage to penetrate more than about 100 km north of the concentrated pack ice edge (e.g., Aars et al. 2009; Frost et al. 2004). As for polar bears, this limited survey effort has resulted

in uncertainty regarding the global population size for ringed seal, which is currently estimated at about 7 million (Davis et al. 2008; Wiig et al. 1999; Reeves et al. 2002).

While the primary productivity of pack ice over deep Arctic waters is presumed to be uniformly low and, thus, unsuitable habitat for seals and other marine mammals (e.g., Fischbach et al. 2009), this assumption is based on very few actual measurements collected over huge distances and time periods (Aars et al. 2008). Ringed seals eat primarily young (1–2-year-old) polar cod (*Boreogadus saida*) that live under the ice, as well as the amphipods and small copepods (shrimp-like invertebrates) that polar cod themselves eat. In shallow waters, ringed seals eat other types of fish in addition to older, benthic-dwelling polar cod (e.g., Born et al. 2004; Finley et al. 1983; Labansen et al. 2007). However, both polar cod and their prey have been found to live under ice of all types, including multiyear and first-year drifting pack ice regardless of the ocean depth (Lønne and Gulliksen 1989). In other words, it is apparent that young polar cod do not require ice that is positioned over shallow, continental shelf waters, and, therefore, neither do ringed seals nor the polar bears that prey upon them. If offshore pack ice over deep water is productive enough for polar cod, it should be suitable for ringed seals and polar bears also. This perspective is important because it vastly expands what biologists consider suitable habitat for a number of arctic marine mammals and explains the ability of this ecosystem to sustain these species over millions of years despite dramatic shifts in ice extent and persistence (e.g., Harington 2008).

The most recent evidence in support of these conclusions comes from a study of genetic diversity in the ringed seal, which showed virtually no regional subdivision across the Arctic (Davis et al. 2008). The authors, in attempting to explain these results, suggest that preferred landfast ice breeding locations for mature ringed seals may be more limited than previously thought and propose that competition for landfast ice breeding territories may drive many ma-

ture seals offshore to breed in the pack ice. This suggests to us an explanation for how and why ringed seal ecotypes develop and persist. If strongly territorial, large bodied individuals of both sexes out-compete weakly territorial, smaller-bodied seals for access to limited coastal breeding habitats, smaller-bodied and more rapidly-maturing animals will end up breeding in the pack ice (see discussions of body size vs. relative growth rates in Crockford 2006). Certainly, within landfast ice habitats, ringed seals of both sexes set up territories during the breeding season (Smith and Hammill 1981; Krafft et al. 2007), and both reportedly show territorial aggression during this time (Smith and Hammill 1981; Stirling 1977, cited in Lydersen and Gjertz 1986). In other species, a strong correlation has been found between body size and degree of territorial aggression, especially in males that stake out breeding territories; in some taxa, these traits appear to be positively linked to variations in plasma testosterone levels (e.g., Sinervo et al. 2000). Thus, strongly territorial behavior and an associated larger body size that allows highly territorial animals to successfully outcompete smaller-bodied individuals for preferred breeding sites may drive continual recruitment of small-bodied seals into the offshore pack ice environment, leading to the development of two ecotypes that are morphological distinct but genetically indistinguishable.

Moreover, a related issue that has important implications for zooarchaeology is the high probability that the ringed seals that breed on coastal shorefast ice are the source of virtually all skeletal specimens of this species held at museums and other institutions because of their increased accessibility. This means that comparative skeletons available in museums may vary widely in size and many collections are likely to be heavily biased toward specimens of the large form. For example, Storå (2000:205) reports "a number of individuals with a very small body size" in his age estimation study of ringed seals collected from the Baltic Sea, although he gives no possible explanation for this phenomenon. Thus, for example, a collecting

bias may account for the fact that virtually all ringed seal specimens that we examined in the National Museum of Natural History (NMNH) collection, Smithsonian Institution, were large enough to overlap in size with small harbor seals. As a consequence, making note of specimen collection location is especially important for this species, although caution is needed: curators may not always distinguish pack ice from shorefast ice collection locations in their records, in part because this information is not routinely provided (see Appendix 4.1 for an example). Landfast breeding populations of ringed seals are virtually the only ones examined by biologists studying pupping and breeding phenomena (e.g., Davis et al. 2008; Holst et al. 1999; Krafft et al. 2006, 2007; Smith and Hammill 1981; Stirling and Øritsland 1995). Although modern Inuit hunters in many areas, such as west Greenland (Finley et al. 1983), and perhaps the Bering and Chukchi Seas as well, probably access pack ice populations during annual harvests, this information seems not to make its way back to research biologists or museum curators.

ZOOARCHAEOLOGICAL ANALYSIS RESULTS

PAGOPHILIC SPECIES

Substantial numbers of bearded and ringed seal remains in the assemblage indicate that spring pack ice reached a more southerly position during the Neoglacial than it does today and persisted until summer. Today, bearded seals in the Bering Sea passively migrate south with the advancing pack ice in spring (Simpkins et al. 2003). This moving ice platform takes animals at the leading edge of the pack quite far south. Females haul out on the ice to give birth from about mid-March to early April (Burns 1970), and pups are nursed for 24 days or less. Adult bearded seals mate after pups are weaned and continue to haul out on the ice during an extended molting period that can last several months, during which time the reced-

ing ice pack usually carries them north. Because juvenile and subadult animals molt in the early spring while mature mammals are giving birth, all age classes of bearded seals may be available when the pack ice is at its full extent.

Similarly, ringed seals in the Bering Sea also move south with the expanding pack ice in the spring (Burns 1970; Simpkins et al. 2003). They haul out to give birth from March through May, with a peak in mid-April (Fedoseev 1975). Most animals continue to spend extensive periods of time on the ice between May and June, when all but young of the year haul out to molt. Young juveniles, including newly weaned young, stay in the water at the ice edge to feed while older animals molt. In the fall, all age classes are usually found together, feeding in open water south of the pack ice or in open polynyas (Born et al. 2004; Holst et al. 1999; Wiig et al. 1999).

BEARDED SEAL REMAINS

Bearded seal remains from the Amaknak Bridge site represent 4% of the total identified sample (264/5947), and while this may seem an insignificant amount, it is substantially more than has been reported from archaeological sites in the Canadian Arctic Archipelago and Greenland. For example, for the mammalian remains (NISP 26,642) reported by Møhl (1979) for the Thule site of Nugarsuk in west Greenland (with species totals adjusted to account for the stated bias in identification effort for small phocids, as per Davis 2001), relative frequencies break down thus: 87% ringed seal, 9% harp seal, 1% bearded seal, 0.4% harbor seal, 0.1% walrus, and 3% other species (such as polar bear, caribou, whale, etc.). Similarly, in a comparison of the marine mammal remains from 61 arctic sites compiled by Maribeth Murray (2008, table 1), only three contained more than 1% bearded seal: *Walakpa* (Barrow, AK, ca. 1500–1100 BP) had 1.5% bearded seal vs. 59.5% *Phoca* sp. (undetermined small seals); *Coldsite* (Devon Island, Canada, ca. 4000 BP) had 4.3% bearded seal vs. 81.5% ringed seal; *Skraeling*

(Ellesmere Island, Canada, ca. 900 BP) had 2.5% bearded seal vs. 66.4% ringed seal.

The only faunal assemblages we found reported in the literature that had frequencies of bearded seal exceeding 4% of the total NISP are reported by Woollett et al. (2000), from three small Thule and historic Inuit sites in Frobisher Bay (south Baffin Island, Canada) that date from the 16th to the early 20th century. NISPs ranged from 110 to 133,and all pinniped species totals were based on counts of auditory bullae, boney palate, maxillae, mandibles, and humeri only. In these sites, bearded seal made up 6–8% of the sample, ringed seal 69–82%, harp seal 2–6%, harbor seal 5–7%, and walrus 4–12%.

Therefore, we conclude that even low percentages of bearded seal remains in an archaeological assemblage are reliable indicators of pack ice habitat. In addition, as bearded seals haul out on pack ice to give birth and nurse their young in early spring, the presence throughout the site assemblage of neonatal (0–3 weeks) and newly-weaned (ca. 4–8 weeks) individuals indicate that the ice edge habitat which bearded seals prefer must have been available close to the Amaknak site thoughout the spring (March–May). The bearded seal sample described here provides substantial evidence that at the height of the Neoglacial, pack ice was probably present off Unalaska Island well into summer on a regular basis.

RINGED SEAL REMAINS

In contrast to bearded seal, ringed seal remains comprised an astonishing 32% of the total NISP (1905/5947) recovered from the Amaknak Bridge site. The bulk of the ringed seal remains (90%) are estimated to have been about 2 to 6 months of age (Crockford et al. 2004), the age class that feeds at the edge of the pack ice during early summer. The very low frequency of adult and neonatal remains suggests little successful hunting for ringed seals took place during the birthing season, and the lack of subadult and older juvenile material argues against the suggestion that ringed seals were

harvested from open water in the fall (where all age classes feed together).

The vast majority of the Amaknak Bridge juvenile remains are also small for their developmental stage, as compared to most juveniles in modern collections (Figure 4.3), which suggests they represent the pack ice ecotype described previously. If pack ice ecotypes are smaller at birth than shorefast ice ecotypes and have faster early growth rates, suture fusion in pack ice juveniles should be further advanced at all ages than shorefast ecotypes. The fact that most of the Amaknak Bridge juveniles are only slightly larger but better developed than the 8-to-12-week-old shorefast ecotype available for comparison (UAM 11633, see Appendix 4.1) supports our interpretation that the Amaknak Bridge ringed seal sample is dominated by pack ice ecotype juveniles aged 3 to 4 months of age (range, 2 to 6 months). The few adult remains recovered are also smaller than adults of modern animals collected from shorefast ice locations, similar in size to the adult female pack ice individual available (UAM 11672, see Appendix 4.1) and typical specimens of Baikal seal (*Phoca sibirica*), the smallest of all phocid seals. Lack of suitable modern samples of known-aged ringed seals (both adult and young juveniles), taken from known pack ice vs. shorefast ice locations, precluded a more detailed analysis. We contend, however, that since Amaknak Bridge bearded seals must represent animals harvested from the edge of late spring/ early summer pack ice habitat, ringed seals were very likely harvested at the same time and thus likely represent the small pack ice ecotype.

We believe that the strong representation in this sample of ringed seals 2 to 6 months of age provides additional evidence that at the height of the Neoglacial, pack ice must have been present off Unalaska Island and persisted well into summer on a regular basis over several centuries, a phenomenon that is unprecedented historically. The small size of the ringed seal skeletal elements, compared to those from comparative specimens of similar developmental stage taken from shorefast ice

FIGURE 4.6. Modern northern fur seal (UVic and RBCM numbers) vs. specimens from La Push, WA (LAP numbers), with estimated or known ages. (A) Humerus, L to R: LAP 224 (fetal); LAP 225 (0–2 wks); LAP 221 92-4 wks); RBCM F80-11 (2 wks). (B) scapula, L to R, RBCM F80-11 (2 wks) vs. LAP 219 (0–2wks). (C) scapula, L to R, UVic 90/140 (6–8 wks) vs. LAP 220 (8–12 wks). (D) femur, L to R, RBCM F80-11 (2 wks); LAP 058 (fetal); LAP 217 (0–2 wks); LAP 215 (2–4 wks); LAP 121 (4–6 wks); UVic 90/140 (6–8 wks). Note that specimens numbered 058 and 121 are from the controlled excavation (undisturbed and dated), the others are from undated disturbed deposits.

habitats, suggests very strongly that ancient Aleut hunters were harvesting the same pack ice ecotype described by modern Inuit hunters and scientific researchers.

TEMPERATE SPECIES: NORTHERN FUR SEAL REMAINS

Substantial numbers of NFS remains were recovered from the Amaknak Bridge site (40% of the total NISP, 2377/5947). Almost half of all NFS remains that could be aged (46%) were subjectively estimated as representing unweaned pups (Figure 4.6), while 28% were judged to be adult or close to adult sized, with epiphyses fused (the line of epiphyseal fusion being absent or just visible). Within this oldest category (NISP 529), 71% (NISP 373) were potentially breeding age adults (adult/subadult), and 84% of these were male, recognizable due to the extreme sexual dimorphism characteristic of this species. Other age classes were poorly represented.

The presence of all age groups and both sexes of NFS, including newborn and still-nursing

infants, provides strong evidence for the presence of pupping grounds in the site vicinity (Crockford et al. 2002; Etnier 2002; Newsome et al. 2007). The presence of unweaned newborns in particular confirms that hunting of NFS occurred, at least part of the time, on breeding rookeries. Today, the primary Bering Sea rookeries are on the Pribolof Islands (Gentry 1998), about 400 km to the north of Unalaska. This is almost certainly farther than residents of the eastern Aleutians could have traveled regularly to hunt. The nearby Aleutian site of Chaluka reported by Etnier (2002) suggests that a fairly substantial rookery must have existed close to the site at the time it was occupied, either on the island of Unalaska itself or somewhere nearby. The presence of a well-established local rookery that no longer exists and was not recorded during the 18th-century commercial sealing boom (Kenyon and Wilke 1953) indicates that the distribution pattern of NFS was very different during the prehistoric period than it is today. We contend that the same expansion of Bering Sea pack ice that brought arctic seals to the doorstep of Amaknak Bridge hunters also made the Pribilofs inaccessible to fur seals during their early summer pupping season (June–July) or rendered them too inclement (due to ice-associated winds) for survival of fur seal newborns (Trites and Antonelis 1994).

ESTABLISHMENT OF NFS ROOKERIES ALONG THE NORTHWEST COAST AND ALEUTIAN ISLANDS

EVOLUTIONARY HISTORY OF NFS ROOKERIES

NFS have the longest evolutionary history of all otariids and have existed in the North Pacific as a discrete lineage for about 25 million years (Arnason et al. 2006). Although it is often assumed that the Pribilof Islands have always been used by NFS as a breeding rookery, during the Last Glacial Maximum of the Pleistocene (and at least once before then), the Pribilofs were part of the Bering Land Bridge and

thus inaccessible to fur seals from at least 25,000 to 11,500 BP (Berta and Sumich 1999; England and Furze 2008; Guthrie 2004). Consequently, even if NFS did not use these islands prior to the onset of the Holocene, the contemporary use of the Pribilofs suggests that fur seal life history strategies are sufficiently flexible to adjust to fairly major disruptions in their migratory habits and preferred breeding environment. The fact that nonmigratory NFS colonies established in southern CA in 1968 are still flourishing today is proof that such life history flexibility still exists (Gentry 1998; Nowak 2003; Peterson et al. 1968; Testa 2007).

The Pribilof Islands would have been exceptionally suitable as rookery habitat for fur seals during the Holocene, since the islands were never occupied by aboriginal people and were too far away from the nearest land masses (at least 400 km) for aboriginal hunters to access from elsewhere (Figure 4.1). Such a refuge from prehistoric hunting pressure makes it extremely doubtful that fur seals failed to utilize the Pribilofs before the Neoglacial period, given that aboriginal populations dependent on marine mammal hunting were already well established in the surrounding region at that time (Knecht and Davis 2001). During the Neoglacial, however, increased winds in the Bering Sea appear to have forced spring pack ice south to the eastern Aleutians, where it persisted well into summer (June/July). The Pribilof Islands almost certainly became more and more unacceptable as a pupping location for NFS from about 4700 BP onward. Although we cannot say for certain that breeding colonies of fur seals existed on the Pribilofs prior to the Neoglacial, we do know that rookeries were established there as soon as Neoglacial conditions ameliorated at about 2700 to 2500 BP, as natural accumulations of fur seal bones dated to that period have been recovered (Etnier et al. 2005).

EVIDENCE OF NONMIGRATORY NFS ROOKERIES

We suggest that the inaccessibility of the Pribilofs from May through July (due to Neoglacial

TABLE 4.2
NFS Measurements from La Push, WA (45CA23)

FAUNAL #	ELEMENT	SIDE	ESTIMATED AGE	GL (MM)
LAP23T206	Femur	R	ca. 24–36 wks	49.7
LAP23T025	Femur	L	ca. 24–36 wks	50.0
LAP23T204	Femur	L	ca. 24–36 wks	50.3
LAP23T205	Femur	R	ca. 24–36 wks	50.4
LAP23T134	Femur	L	ca. 24–36 wks	53.2
LAP23T095	Femur	R	ca.24–36 wks	54.9
LAP23T211	Femur	R	ca. 8–12 wks	44.4
LAP23T057	Femur	L	ca. 8–12 wks	46.1
LAP23T005	Femur	R	ca. 8–12 wks	44.0
LAP23T209	Femur	R	ca. 8–12 wks	44.5
LAP23T003	Femur	L	ca. 8–12 wks	45.3
LAP23T026	Femur	L	ca. 6–8 wks	35.8
LAP23T002	Femur	L	ca. 6–8 wks	40.2
LAP23T001	Femur	L	ca. 6–8 wks	41.1
LAP23T207	Femur	R	ca. 6–8 wks	41.8
LAP23T210	Femur	R	ca. 6–8 wks	41.8
LAP23T004	Femur	R	ca. 6–8 wks	42.1
LAP23T024	Femur	R	ca. 6–8 wks	42.3
LAP23T212	Femur	R	ca. 6–8 wks	42.4
LAP23T121	Femur	L	ca. 6–8 wks	42.7
LAP23T213	Femur	R	ca. 6–8 wks	43.4
LAP23T008	Femur	R	ca. 2–6 wks	28.9
LAP23T022	Femur	R	ca. 2–6 wks	29.5
LAP23T007	Femur	R	ca. 2–6 wks	30.5
LAP23T023	Femur	R	ca. 2–6 wks	31.4
LAP23T216	Femur	L	ca. 2–6 wks	32.7
LAP23T010	Femur	L	ca. 2–6 wks	32.7
LAP23T009	Femur	L	ca. 2–6 wks	33.1
LAP23T215	Femur	R	ca. 2–6 wks	33.4
LAP23T218	Femur	R	< 0–2 wks	24.2
LAP23T011	Femur	L	< 0–2 wks	26.5
LAP23T006	Femur	R	< 0–2 wks	26.8

TABLE 4.2 *(continued)*

FAUNAL #	ELEMENT	SIDE	ESTIMATED AGE	GL (MM)
LAP23T217	Femur	L	<0–2 wks	27.1
LAP23T058	Femur	R	<0 wks (fetal)	21.4
LAP23T177	Humerus	L	ca. 8–12 wks	59.2
LAP23T096	Humerus	L	ca. 6–8 wks	52.5
LAP23T222	Humerus	L	ca. 2–6 wks	39.0
LAP23T020	Humerus	L	ca. 2–6 wks	41.5
LAP23T221	Humerus	R	ca. 2–6 wks	42.4
LAP23T226	Humerus	L	<0–2 wks	31.3
LAP23T225	Humerus	R	<0–2 wks	35.8
LAP23T133	Humerus	R	<0–2 wks	37.2
LAP23T224	Humerus	R	<0 wks (fetal)	25.6
LAP23T191	Radius	R	ca. 8–12 wks	69.0
LAP23T229	Radius	R	ca. 6–8 wks	63.3
LAP23T021	Radius	R	ca. 2–6 wks	39.3
LAP23T228	Radius	R	ca. 2–6 wks	43.1
LAP23T013	Radius	R	ca. 2–6 wks	43.6
LAP23T012	Radius	R	<0–2 wks	35.7
LAP23T227	Radius	L	<0–2 wks	38.7
LAP23T015	Radius	R	<0 wks (fetal)	23.5
LAP23T014	Radius	R	<0 wks (fetal)	24.7
LAP23T016	Radius	L	<0 wks (fetal)	30.2

NOTE: Specimens numbered T001–T191 were recovered during controlled excavation of intact and dated deposits, while those numbered T200–T228 were recovered during backdirt screening of disturbed deposits.

pack ice expansion) was likely the event that prompted fur seals to establish nonmigratory breeding colonies along the Aleutian Archipelago and the west coast of North America, as documented by numerous zooarchaeological studies (Crockford et al. 2002; Gifford-Gonzalez et al. 2005; Moss et al. 2006). While these published accounts are convincing, however, they are not the only examples that exist: many other recently-excavated sites on the Northwest Coast and throughout the Aleutians, especially those sub-ject to small-scale excavations and described in unpublished accounts, continue to yield evidence of nonmigratory NFS rookeries.

We report here previously unpublished measurements (Table 4.2) and comparative photos (Figure 4.6) of some very young NFS long bones recovered from one such site, a salvage recovery on the west coast of the Olympic Peninsula, WA (Wessen 2006). This late prehistoric site was occupied during a narrow time period somewhere between ca. 600 to 1000 BP (two C[14]

dates are reported: 880 ± 50 and 660 ± 50, from the top and bottom of excavated deposits, respectively). Recovery efforts at the site generated faunal remains from a 2 × 2-meter excavation in an intact portion of the site, where the mammalian component was found to be heavily dominated by NFS remains of all age classes, including adults and very young pups (93% of the total NISP 1130). A few additional NFS remains were recovered during screening of backdirt from a disturbed portion of the site. The youngest of these remains indisputably represent unweaned pups, which represent the strongest evidence available that local rookeries attended by nonmigratory NFS were being harvested by aboriginal hunters.

WHY AND WHEN NONMIGRATORY ROOKERIES WERE ESTABLISHED

While decimation of prehistoric Aleutian and Northwest Coast colonies can quite reasonably be attributed to a combination of aboriginal and European hunting practices (e.g., Gentry 1998; Newsome et al. 2007), no one before this time has suggested an explanation for why such rookeries would have been established in the first place during the Middle Holocene, nor why these colonies were composed of nonmigratory animals. We contend that pack ice expansion at the beginning of the Neoglacial encouraged some fur seals, especially those with relatively weak migratory instincts and/or natal site fidelity, to establish new rookeries throughout the eastern North Pacific. Many of these new rookeries were very successful and survived well into the historic period (e.g., Crockford et al. 2002). Individuals with strong migratory instincts and powerful natal site fidelity probably become relatively rare during the Neoglacial. Reinvasion of the Pribilof Islands could only have occurred after the climate ameliorated, when individuals with strong migratory instincts would again have had an evolutionary advantage, given their unique ability to utilize this seasonally available rookery location that is so well protected from human harvest. Therefore, the currently dominant life history pattern of NFS, where virtually all breeding and pupping take place on the Pribilofs in June and July, after which females and juveniles migrate south to feed over the winter, is one of at least two strategies available to this species.

CONCLUSIONS AND DISCUSSION

The zooarchaeological data from the Amaknak Bridge site provides evidence that for about 2000 years during the mid-Holocene, seasonal pack ice in the Bering Sea extended farther south and persisted longer, on a regular basis, than it does today. While significant climatic cooling during the Neoglacial is known to have occurred, this is the first evidence for such a dramatic increase in Bering Sea pack ice during this period (Crockford and Frederick 2007). The comprehensive skeletal analysis described here provides two excellent examples of how animal life history flexibility can be ascertained from zooarcheolgical material: for one species, this flexibility was known about but not recognized as being especially important and the other species had a flexibility not previously appreciated before zooarchaeological analysis provided the evidence.

The first example, that two distinctly sized ecotypes of ringed seal exist, had been discussed by biologists for decades but was largely dismissed as a minor ecological and life history feature. However, a somewhat tentative conclusion that pack ice–breeding seals must make up a significant portion of the global population is now supported by phylogenetic evidence, and this has implications for both archaeologists and biologists. Combined with the knowledge that ancient Inuit hunters probably harvested large numbers of ringed seals from the southern edge of the Arctic pack ice, we suggest that assemblages of ringed seals from other prehistoric Arctic sites may also contain large numbers of small-sized, pack ice seals and perhaps should be re-analyzed (e.g., Woollett et al. 2000, who remarked on small seals from the Labrador component of their site material). Biologically speaking, having two life

history strategies—one that utilizes shorefast ice and another that takes advantage of mobile pack ice—has almost certainly given ringed seals the evolutionary flexibility they have needed to survive in the Arctic over millions of years; such flexibility certainly needs to be factored into modern ecological studies and population estimates.

Our second example challenges the notion that current distributions and life history strategies of NFS in the North Pacific have been in place throughout the Holocene (e.g., Reeves et al. 2002). If we accept the assumption that the Pribilof Islands were utilized by NFS as summer rookeries in the Early Holocene, then Neoglacial sea ice expansion explains the post-Middle Holocene dates for the establishment of local rookeries throughout the Aleutian Archipelago and the Northwest Coast. Although archaeological sites older than ca. 5000 BP are admittedly rare in the eastern North Pacific, no sites that predate ca. 4700 BP have yet been reported that show evidence of nonmigratory NFS rookeries (Gifford-Gonzales et al. 2005). If the Pribilofs did not host NFS rookeries during the Early Holocene, then the current life history pattern of this species, where 99% of the population gives birth in the Bering Sea to offspring that are weaned by 4 months of age, was established less than 200 years ago when the last well-established rookeries of nonmigratory animals were wiped out. If so, a pattern may have existed for the 2300 years prior (and at other times in their history), whereby the entire NFS population was composed of both migratory and nonmigratory subgroups. Unfortunately, we simply do not have enough evidence at this time to determine which of these options is correct.

Both of these examples remind us that many species are more flexible and adaptable in their life history strategies than conventionally thought and that zooarchaeological data can be an invaluable addition to contemporary biological and ecological studies that attempt to explain such differences. Since life history flexibility may be what has allowed both ringed seals and NFS to persist over millions of years and countless shifts in environmental conditions, evidence of life history flexibility ascertainable from the zooarchaeological record is as important to biologists as it is to archaeologists.

ACKNOWLEDGEMENTS

Phocid Seal Comparative Skeletons Used for Estimating Age and Species Determination

SEAL	GENDER	DATA
P. vitulina		
UVic 85-8	-	(stillborn? < 1 wk)
UVic 97/42	-	(newborn, ca. 1 wk)
UVic 88/124	-	(newborn, ca. 1 wk)
UVic 86/85	-	(subadult)
UVic 84/48	-	(subadult)
P. largha		
UAM 16605	F	(unweaned, ca. 2–4 wks)[a]
NMML 196	F	skull (ca. 8–12 wks)[c]
BM 34221	M	(juvenile/subadult)[c]
UAM 11676	F	(adult, mother to 16605)[a]
UAM 11675	M	(adult? mate of 11676)[a]
NMML 402	M	skull (adult/subadult)[b]
P. hispida		
UAM 11581	F	(weaned, ca. 6–8wks)[a]
UAM 11633	M	(ca. 8–12 wks)[d]
NMNH 504210	-	(ca. 8–12 wks)[d]
NMNH 504214	-	(juvenile)[d]
UAM 11672	F	(adult/subadult)[a]

SEAL	GENDER	DATA
NMNH 7102	-	(adult)[d]
NMNH 305081	M	(adult/subadult)[d]
P. fasciata		
UAM 16619	M	(unweaned, ca. 3–4 wks)[a]
UAM 11529	M	(weaned, ca. 6–8 wks)[a]
UAM 11469	M	(subadult/adult)[a]
E. barbatus		
NMNH 16112	F	(fetus, at/near term)[c]
NMNH 550412	-	(weaned, ca. 6–8 wks)[c]
BM 34219	-	(juvenile)[c]
NMNH 16116	F	(adult/subadult)[c]
NMNH 550250	F	(adult/subadult)[c]
NMNH 550251	F	(adult/subadult)[c]

[a] Indicates collection known from pack ice habitat.
[b] Indicates ice habitat unknown.
[c] Indicates collection presumed to be from pack ice habitat.
[d] Indicates collection presumed to be from shorefast ice habitat.
INSTITUTIONAL DESIGNATORS: UVic, University of Victoria, Anthropology; UAM, University of Alaska Museum, Fairbanks; NMML, National Marine Mammal Laboratory, Seattle; NMNH, National Museum of Natural History, Washington DC; BM, Burke Museum, Seattle.
NOTE: Age estimates given for juveniles < 1 yr are based on a combination of collection notes, collection dates, and mean dates of birth for that taxa. General age estimates for animals > 1 yr are based on collection date and epiphyseal fusion, such that unfused epiphyses and smaller than adult size are "juvenile," fused or partially fused epiphyses with suture lines evident, close or equal to adult size is "subadult," while those with fused epiphyses and no suture lines evident are "adult." UAM 11581 (*P. hispida*) and UAM 11529 (*P. fasciata*) were collected in April 1963 by a research team working out of Gambell, St. Lawrence Island, within days of each other. Since the unweaned *P. fasciata* pup was almost certainly taken from pack ice, we presumed that the *P. hispida* specimen was also, especially as the occurrence of ringed seal "whitecoat" pups and breeding females in the pack ice were noted in the study (Burns 1970).

Northern Fur Seal Comparative Skeletons Used for Estimating Age of Young Pups, All from Rookeries on the Pribilofs, Alaska

SEAL	GENDER	DATA
RBCM F80/11	-	(unweaned, ca. 0–2 weeks)
UVic 90/141	M	(unweaned, ca. 5–6 weeks)[a]
UVic 90/140	F	(unweaned, ca. 6–8 weeks)[a]
UVic 87/26	M	(weaned, 6–8 month)

[a] Sex designated here corrected from Crockford et al. 2002.
INSTITUTIONAL DESIGNATORS: UVic, University of Victoria, Anthropology; RBCM, Royal B.C. Museum, Victoria.

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