

# Evaluating Cementum to Determine Past Reproduction in Northern Sea Otters

VANESSA R. VON BIELA,<sup>1</sup> Department of Biological Sciences, University of Alaska Anchorage, 3211 Providence Drive, Anchorage, AK 99508, USA

J. WARD TESTA, National Marine Mammal Laboratory, Alaska Fisheries Science Center, c/o Department of Biological Sciences, University of Alaska Anchorage, 3211 Providence Drive, Anchorage, AK 99508, USA

VERENA A. GILL, Marine Mammals Management, United States Fish and Wildlife Service, 1011 E Tudor Road, Anchorage, AK 99503, USA

JENNIFER M. BURNS, Department of Biological Sciences, University of Alaska Anchorage, 3211 Providence Drive, Anchorage, AK 99508, USA

**ABSTRACT** Age at first reproduction (AFR) has been difficult to quantify in mammals, as the most commonly used methods require reproductive tracts or direct observations. However, work in several large mammal species suggests that the width of cementum light bands in teeth decline once females begin to reproduce, suggesting that teeth structures might provide a new tool to examine AFR. To determine if changes in cementum light band width could be used to calculate AFR for the northern sea otter (*Enhydra lutris kenyoni*), we measured cementum light band widths on sectioned premolar teeth and compared them to reproductive tracts. We classified otters as parous if any single light band was narrower than a threshold value, selected as the value that minimized error rates. At a threshold value of 0.32, we correctly identified otters as parous or nulliparous in 83% of cases ( $n = 92$ ) as compared to reproductive tracts, and the AFR estimated from teeth samples ( $3.52 \pm 0.032$  yr) was not different from that determined by reproductive tract analysis ( $3.45 \pm 0.031$  yr;  $t$ -test,  $P > 0.05$ ). These data support the use of cementum as an indicator of past reproduction in individual female otters, which can then be used to estimate average AFR. Given that declines in cementum width have been described for other mammal species, the same quantitative approach used here could be applied to other species. (JOURNAL OF WILDLIFE MANAGEMENT 72(3):618–624; 2008)

DOI: 10.2193/2007-218

**KEY WORDS** age at first reproduction, Alaska, cementum width method, demography, *Enhydra lutris*, population biology, reproduction, sea otter.

Environmental factors such as density, predation, and nutrition directly impact individual fitness by influencing the net energy gain of an individual (Stearns 1976). Life-history theory predicts that individuals should adjust the energy allocated to reproduction to maximize fitness. For example in dense, resource-limited populations, individual fitness may be maximized by delaying the individual's age of first reproduction (iAFR) if it sufficiently increases survival (Bengtson and Laws 1985, Skogland 1985, Choquenot 1991, Festa-Bianchet et al. 1995). Similarly, when population declines are driven by bottom-up causes, such as resource limitation, the average AFR (aAFR, the population-wide average of iAFRs) for the population will increase, even if some individuals do not delay iAFR (Stearns 1976, McMahon et al. 2003). In contrast, when population declines are driven by top-down forces, such as predation, resources are usually abundant and aAFR tends to decrease as more females begin reproducing at younger ages (Dzikowski et al. 2004). Therefore, changes in both iAFR and aAFR may provide insight to underlying causes of population declines (Eberhardt and Siniff 1977, Bengtson and Laws 1985).

Unfortunately, because estimating aAFR for a population entails determining the iAFR for a large number of known-age females, it is rarely measured (Boness and James 1979, Clutton-Brock 1988, Testa et al. 1990, Le Boeuf and Reiter 1991). In large mammals iAFR is often determined through long-term mark-recapture or monitoring studies that are time-intensive, expensive, and logistically difficult due to the

long time period over which they must be carried out (Testa et al. 1990, Siniff and Ralls 1991, Monson et al. 2000, Pistorius et al. 2001). These studies become particularly problematic for species or populations where there is high tag loss, high mobility, or low site fidelity.

An alternate method for estimating iAFR is the use of reproductive tracts, which contain indicators of current and past pregnancy (corpora lutea [CLs] and corpora albicantia [CAs], respectively; Bodkin et al. 1993, Stirling 2005). If the minimum time a CA persists in the ovary and the youngest possible age of first ovulation is known, then the iAFR can be back-calculated using the individual's age and exact number of past reproduction indicators. In this method, total number of CLs and CAs are subtracted from the individual's age to arrive at iAFR, provided that the female is younger than or equal to the minimum iAFR plus the minimum number of years CAs persist in the ovary (Bengtson and Siniff 1981). However, this technique cannot be used to calculate iAFR if either the minimum iAFR or the minimum CA persistence is unknown or highly variable.

However, assumptions of the back-calculation method are relaxed if ovarian structures are used only to determine whether an individual has reproduced by the time of sampling, as indicated by the presence of a CA. Then, the proportion of females that have reproduced in each age class can be used to calculate an aAFR for the population following methods outlined by DeMaster (1978). However, utilizing this technique requires an appropriate sample size and age distribution, preferably  $\geq 25$  females per age class from the youngest age at which any female can begin reproducing until the age that all females become repro-

<sup>1</sup> E-mail: [vvonbiela@usgs.gov](mailto:vvonbiela@usgs.gov)

ductive (DeMaster 1978). Although analyzing reproductive tracts is neither expensive nor time-intensive, it is destructive, making collection of such a large stratified sample difficult or prohibited due to management concerns.

Whether using reproductive tract analysis to estimate iAFR or aAFR, the individual's age must be known. In mammals, dental cementum annuli are widely used in age estimation because the alternating pattern of light bands and dark annuli is easily distinguishable using transmitted light (provided the tooth was not subject to excessive mechanical stress). Each year a wide transparent layer, the light band, and a narrow dark layer, the annuli, are laid down around the outside of the tooth within the gums. In many temperate species the light band is formed from late spring to early autumn, the part of the year associated with higher growth, and the dark annulus is formed from late autumn to early spring, a time associated with lower growth (Klevezal and Kleinenberg 1969). Light bands and annuli are not reabsorbed like bone, or restricted by pulp cavity volume like dentin, and researchers regularly collect teeth from captured animals (Klevezal and Kleinenberg 1969, Klevezal 1996, Stewart et al. 1996, Bodkin et al. 1997). Thus, the number of annuli provides an index of animal age, and the width of the light bands is thought to be related to intrinsic and extrinsic factors that influence seasonal growth rates. An additional common feature in many mammalian teeth is the decline in cementum light band width with age (Klevezal and Kleinenberg 1969, Craighead et al. 1970, Bengtson and Siniff 1981, Klevezal and Stewart 1994), which has been attributed to sexual maturation (iASM, age when pregnancy becomes possible) or initiation of reproductive activity in females (iAFR; Coy and Garshelis 1992, Klevezal 1996), which suggests that changes in light band width may provide an alternative method for identifying reproductive status. Indeed, researchers have shown that the age at which cementum light band width declines (determined visually) is correlated with iAFR or iASM as determined from reproductive tracts or mark-recapture analyses in ringed (*Phoca hispida*), gray (*Halichoerus grypus*), crabeater (*Lobodon carcinophagus*), and northern elephant seals (*Mirounga angustirostris*; Soderberg 1978, Bengtson and Siniff 1981, Klevezal and Stewart 1994). In addition, Coy and Garshelis (1992) found that narrow light bands were laid down during cub-rearing events in black bears (*Ursus americanus*). In contrast Baker and Boveng (1997) failed to find a strong correlation between iAFR and light band width decline in harbor seals (*Phoca vitulina*). Similar declines in light band widths also might occur in males, but these patterns have not been studied because female reproductive parameters limit population dynamics more often than do male reproductive parameters.

Although cementum measurements may not reliably pinpoint iAFR for all species, it might be possible to use changes in light band width to determine if a female is parous (having given birth) or nulliparous (not yet reproductive). If so, then cementum analyses could provide the data necessary to estimate aAFR for a population

following the DeMaster (1978) calculations discussed above. Recent declines in northern sea otter populations (*Enhydra lutris kenyoni*) in southwest Alaska have focused interest on development of new methods for estimating life-history parameters that influence population trajectories. Because sea otters may reproduce more than once per year, and the minimum time that an ovarian structure remains visible in the ovary is unknown, we could not use the back calculation method to obtain iAFR from reproductive tracts for comparison to cementum measurements (Bodkin et al. 1993). Instead, we tested whether cementum light band measurements could be used as an indicator of past reproduction in northern sea otters.

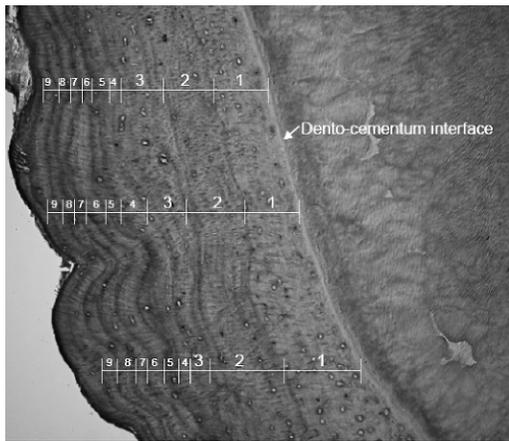
## STUDY AREA

We collected reproductive tracts and premolar teeth from 92 female northern sea otters between the ages of 2 years and 14 years old from 1989 to 2005. Northern sea otters are a subspecies of sea otter distributed along the Aleutian Islands (southwest AK) to Oregon, USA (Wilson et al. 1991). Samples were available from 3 sources: carcasses collected as a result of the 1989 Exxon Valdez Oil Spill (United States Geological Survey [USGS] and United States Fish and Wildlife Service [USFWS];  $n = 42$ ), stranded otters that likely died from acute causes collected between 1994 and 2005 in Alaska ( $n = 17$ ) and Russia ( $n = 4$ ; USFWS), and subsistence-hunted otters collected across Alaska (The Alaska Sea Otter and Steller Sea Lion Commission and USFWS;  $n = 29$ ). We performed all sample collection in accordance with USFWS regulations.

## METHODS

### Cementum Age and Width Analysis

From each female otter, 2 decalcified mid-sagittal longitudinal sections from one premolar tooth were available. We used the first premolar present (PM2, because PM1 is absent in the species) for all analyses, but we did not standardize tooth position (upper or lower). All slides were prepared and aged by Matson's Laboratories (Milltown, MT, USA) as described by Bodkin et al. (1997). We accepted ages determined at Matson's Laboratory and did not attempt to assign independent ages because the Laboratory has been used for sea otter age analysis in all recent studies cited here and G. Matson personally ages all sea otter teeth to maintain consistency (G. Matson, personal communication). To limit possible errors associated with age assignment, we used only results with an age certainty code of A or B (possible error judged to be  $\pm 0$  yr and  $\pm 1$  yr, respectively, for otters 0–7 yr; G. Matson, personal communication). Following staining and age determination, we examined teeth sections at 100 $\times$  magnification and photographed them using a Nikon Eclipse E400 microscope outfitted with a MicroPublisher 3.3 digital camera (QImaging, Burnaby, BC, Canada). We measured width of each light band between the centers of adjacent dark annuli on digital images (Fig. 1) using MetaVue 6.1 (Molecular Devices, Sunnyvale, CA). For each otter, we measured



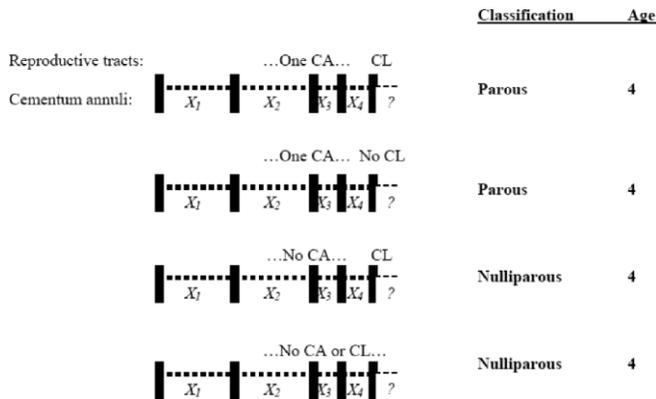
**Figure 1.** Premolar cementum annuli of an adult 9-year-old female sea otter (specimen 480001) from Alaska, USA, in 2005. We took measurements at 3 sites on each of 2 premolar sections.

cementum light band width at 3 variable locations, which we chose based on cementum clarity, on each of the 2 tooth sections for a total of 6 measurements per light band. We measured only completed light bands (large light area bounded by narrow dark annuli), because width of the last incomplete light band would likely be affected by date of death.

We standardized individual light band widths ( $a_{i,n}$ , where  $i$  = measurement site and  $n$  = light band no.) to the widest light band width at each measurement site (or  $a_{i,n} / a_{i,L}$  where  $L$  = largest light band) because cementum light band width is generally thicker closer to the root tip, and that total thickness increases with age, whereas light band thickness decreases with age (Craighead et al. 1970). We compared standardized cementum measurements for each light band by tooth section and measurement site using a repeated measures 2-way analysis of variance to verify that measurements did not vary significantly between measurement site or slide section. Because we detected no significant differences by site or section ( $P > 0.05$ ) we calculated the average of the standardized measurements for each light band, which resulted in one series of average standardized light band width measurements for each otter. We then used the thinnest average light band ( $\bar{a}_{\min}$ ) for each otter in subsequent analyses, provided that the thinnest average band was not the first light band ( $n = 3$ ). If the thinnest light band was the first, we used the next thinnest light band as  $\bar{a}_{\min}$ . We did not use the first light band as  $\bar{a}_{\min}$  because otters do not reproduce in their first year of life (Kenyon 1969, Bodkin et al. 1993). The first light band was the narrowest in these few otters likely because these otters were born late in the season and had little time to growth before the winter season when the dark band was deposited.

### Reproductive Tract Analysis

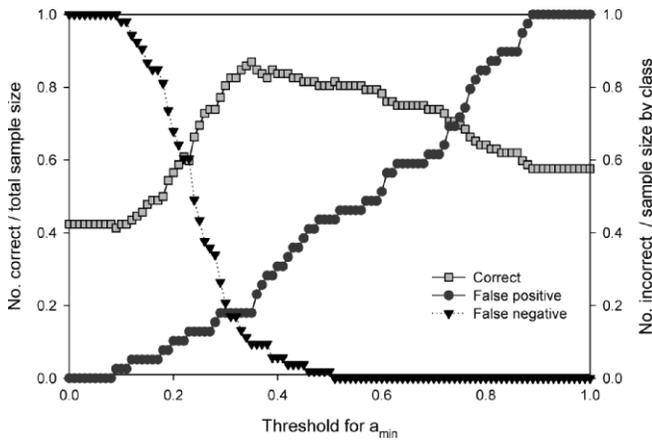
We either immediately fixed reproductive tracts from each otter in 10% neutral buffered formalin or froze them at  $-20^{\circ}\text{C}$ , in which case we thawed and fixed them once formalin was available. All samples remained in formalin for



**Figure 2.** Diagrammatic representation of light band measurement and reproductive tract analysis timelines used for sea otters collected in Alaska, USA, 1989–2005. Each dashed black line represents a tooth from an individual otter. Solid black lines represent the dark cementum annuli bands or years. The space between each solid black line represents the light band width for a given year,  $X_i$ , where  $i$  = year of life. The 4 possible results from reproductive tract analysis are displayed above each dashed line with corpora albicantia (CA) representing the marker of past pregnancy and corpora luteum (CL), the marker of current pregnancy. Ellipses on either side of reproductive tract information indicate that the CL or CA could have formed during any of the light bands listed below. To the right of each dashed line, the resulting reproductive classification and age (yr) we used in the analysis of average age of first reproduction by age class (AFR<sub>tract</sub>) is listed.

$\geq 1$  month prior to analysis. To determine total number of CLs and CAs, we excised fixed ovaries from the reproductive tract, sectioned them by hand at 1–2-mm intervals, and examined them macroscopically (Sinha et al. 1966, Bodkin et al. 1993). For each otter we recorded age and number of CAs and CLs. If reproductive tract analysis returned biologically implausible samples (e.g., reproductive 1-yr-olds) we removed samples from all analyses ( $n = 2$ ).

To compare data from reproductive tracts to changes in cementum widths, this analysis had to account for the fact that each tissue represents a slightly different timeframe in the life of an individual otter. Reproductive tracts contain information on pregnancies up to time of death, whereas cementum measurements capture information only up to the end of winter prior to death, because measurements can only be made on complete light bands (Bodkin et al. 1997). Therefore, to standardize temporal comparisons, we used only data on past pregnancies, as indicated in reproductive tracts by CAs. As a result, these comparisons do not include information on reproductive history in the year of collection. For example, we would treat a 5-year-old otter that was pregnant at time of collection (CL in reproductive tract), but had no signs of past pregnancies (no CAs), as a nulliparous 4-year-old for analyses (Fig. 2). After making these adjustments to reproductive tract data, we determined the proportion of females in each age category that had signs of past reproduction (CAs) for otters ranging in age from 1 year to 7 years. We then used the proportion of parous females in each age class to calculate an aAFR (aAFR<sub>tract</sub>) following DeMaster (1978). Although otters do not reproduce during their first year of life, their inclusion in the calculation improves aAFR estimate and reduces



**Figure 3.** Proportion of females correctly classified as parous or nulliparous (left axis) as well as proportion of false positive and false negative results (right axis) for each possible threshold value of  $\bar{a}_{\min}$ , as determined at 0.01 intervals for sea otters collected in Alaska, USA, 1989–2005.

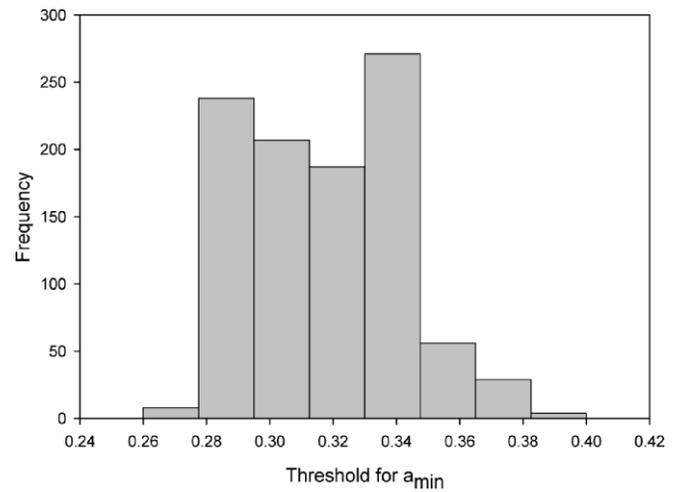
variance. All protocols were approved by the Institutional Animal Care and Use Committee at the University of Alaska Anchorage (IACUC No. 2006burns8).

### Data Analysis

We evaluated use of  $\bar{a}_{\min}$  as an accurate indicator of reproductive status (parous or nulliparous) in 2 ways. In the first analysis we directly compared results from  $\bar{a}_{\min}$  with reproductive tract analysis without regard to age. The objective of this first comparison was to determine a threshold value of  $\bar{a}_{\min}$  that would accurately place otters into the correct reproductive category, nulliparous ( $\bar{a}_{\min} >$  threshold) or parous ( $\bar{a}_{\min} \leq$  threshold), as determined from reproductive tract analysis. We evaluated all possible threshold values of  $\bar{a}_{\min}$  (0.01 to 1.00), with optimal threshold value being that which minimized proportion of false positive ( $\bar{a}_{\min} \leq$  threshold but no indication of prior reproductive events in the tract) and false negative ( $\bar{a}_{\min} >$  threshold but indication of a prior reproductive event in tract) errors by class (parous or nulliparous). We minimized errors by reproductive class to ensure that proportion of otters that were parous in the sample set did not influence the threshold.

To examine variability in the optimal threshold that we would expect in future analysis of sea otter cementum light band measurements, we attained 1,000 bootstrap replicates of the optimal threshold value in the same manner as above (Efron 1982). If a bootstrap replicate returned multiple values for the optimal threshold (e.g., an  $\bar{a}_{\min}$  of 0.33 and 0.34 produced the same results), we used the mean value for the replicate ( $\bar{a}_{\min} = 0.335$ ).

Once we selected the optimal threshold value of  $\bar{a}_{\min}$  from the median of the bootstrap replicates, we used it to classify all otters as parous or nulliparous. We then used the proportion of females in each age that were reproductive to calculate the  $aAFR_{\text{teeth}}$ , the same way we calculated  $aAFR_{\text{tract}}$  (DeMaster 1978). We report means as  $\pm$  standard error. We compared the 2 resulting estimates of  $aAFR$  using a modified  $t$ -test (DeMaster 1978). In addition, we



**Figure 4.** Distribution of the optimal  $\bar{a}_{\min}$  determined from 1,000 bootstrap replicates of a dataset of 92 female sea otters collected in Alaska, USA, 1989–2005. The median optimal threshold value was  $0.32 \pm 0.024$  (median  $\pm$  SD).

calculated expected detectable difference between  $aAFR_{\text{teeth}}$  and  $aAFR_{\text{tract}}$ , from equation 9 in DeMaster (1978).

## RESULTS

We determined the optimal threshold value for  $\bar{a}_{\min}$  to be 0.32 of the largest light band width (Fig. 3). At this optimal threshold value, we correctly classified 83% of samples as parous or nulliparous, the false positive rate was 7.6% (we misclassified 18% of 39 nulliparous samples as parous), and the false negative rate was 10% (we misclassified 17% of 53 parous samples as nulliparous). Neither the false negative nor the false positive error rates were centered around the threshold value; instead, errors were distributed along the entire continuum of possible threshold values. However, results of 1,000 bootstrap replicates gave a narrow estimate of the threshold value:  $0.32 \pm 0.024$  (median  $\pm$  SD; Fig. 4).

After applying the threshold obtained from the median of the bootstrap replicates to each sample, we calculated  $aAFR_{\text{teeth}}$  to be  $3.51 \pm 0.032$  ( $\bar{x} \pm$  SD) years whereas reproductive tract analyses produced an  $aAFR_{\text{tract}}$  of  $3.45 \pm 0.031$  years. The  $aAFR_{\text{teeth}}$  did not differ from  $aAFR_{\text{tract}}$  ( $t_{81} = 1.43$ ,  $P > 0.05$ ) and the calculated detectable difference between means was 0.77 years. Approximately 90% of samples fell in the critical age range (or the range of ages beginning at the last age where no otter were parous to the first age where all otter were parous, 1–7 yr old in our study) for determining  $aAFR$ .

## DISCUSSION

We took a quantitative approach to evaluating cementum light bands as an indicator of past reproduction and found that we could use decreases in cementum width of the light bands between annuli as an indicator of past reproduction in northern sea otters. By selecting an appropriate threshold of cementum light band width, we could correctly identify

most otters as parous or nulliparous, which allowed us to calculate from teeth measurements an aAFR that did not differ from that estimated from reproductive tracts. Our success likely comes from 2 innovations: use of quantitative, not qualitative, measures of cementum and use of cementum light band width to estimate parous status and not iAFR or sexual maturity.

Previous studies linking cementum band width and reproductive events have relied upon an observer's ability to visually identify the age when light cementum bands narrow. Such a method is subjective and particularly prone to errors when examining teeth from animals near the age when the width between cementum annuli decreases (Bengtson and Laws 1985, Baker and Boveng 1997). Here, we used quantitative measurements to determine whether and to what degree light band width changed with parous status. In addition, because there were no significant differences in light band width due to measurement site or slide section, we made light band width measurements at the clearest area of the tooth slides.

A second strength of our study was that we only used the decline in cementum light band width to estimate parous status and not to identify iAFR, which was necessary because annual pregnancy rates and multiyear persistence of ovarian structures are not known for sea otters, making it impossible to determine the  $iAFR_{\text{tracts}}$  needed for comparative purposes. Even if it were possible to determine  $iAFR_{\text{tracts}}$ , estimating  $iAFR_{\text{teeth}}$  likely would have introduced additional sources of error because one might have assumed that the narrowest light band represented  $iAFR_{\text{teeth}}$ , which may or may not have been the case.

One of the difficulties in assigning iAFR based on light bands between annuli is that the exact cause of the decline in width is not known. Although many researchers attribute the decline in cementum light band width to diversion of energy away from growth for support of pregnancy and lactation, others postulate that it is due to endocrine shifts that occur at the onset of sexual maturity, which will occur earlier than the first reproductive event (Klevezel and Myrick 1984, Coy and Garshelis 1992, Klevezel 1996). It is interesting that annual growth increments in fish otoliths (ear stones), similar to cementum in mammals, are often found to be directly proportional to somatic growth (Francis 1990). In sea otters, bands likely narrow because of energetic constraints late in pregnancy and during lactation, but hormonal influences cannot be ruled out. However, by focusing only on whether the light band had narrowed sufficiently to indicate a prior reproductive event, error from this source was less likely.

Solely using decreases in light band width properly classified otters as parous or nulliparous in 83% of cases, evenly distributed misclassifications across both reproductive classes, and spread errors along the possible threshold values, which suggests that misclassifications are not due solely to the selection of  $\bar{a}_{\text{min}}$  but instead may be due to errors in light band measurements, age estimation, or reproductive tract analysis. Errors in age determination or

light band width measurements could have been due to presence of compound or indistinct annuli, but multiple measurements of 2 separate tooth sections likely minimized these errors. However, we could not separate or quantify errors due to age assignment and parous status. We could also have misclassified individual otters if they were able to maintain thick cementum light band widths during pregnancy due to abundant food resources (false negative) or if resource limitations produced narrow bands in nonreproductive individuals (false positives), but we cannot assess prevalence of this source of error. Given the wide variety of environmental conditions likely experienced by otters in our study due to diversity of sampling sites and time periods, the low error rate in our study suggests that changes in light band width associated with parous status are larger than those associated with changing environmental conditions alone. Additionally, by standardizing measurements to the widest light band we designed our analysis to detect a proportional change in light band width for a given individual so that a nulliparous otter experiencing slow growth due to environmental stressors throughout its life, presumably represented as a series of narrow bands, would not have shown a proportional decline in light band width necessary to be classified as parous. Finally, if we overlooked a CA during reproductive tract analysis, we might have falsely classified the otter as nulliparous; alternatively, a detected CA that did not result in a successful pregnancy or a reduction in light band width might result in a false negative. None of these possible sources of error are unique to our study but instead exist in all analyses of reproductive tract data.

Additional support for the use of a minimum cementum light band width measurement ( $\bar{a}_{\text{min}}$ ) as a robust indicator of parous status comes from analysis of the bootstrap results. Not only was the range of optimal  $\bar{a}_{\text{min}}$  produced by the bootstrap replicates narrow, but the median of the bootstrap replicates was identical to that we determined for the original sample. The agreement between the bootstrap median and the optimal threshold value supports the use of this point threshold in future studies of sea otter parous classification. Although a moot point for our study because the optimal threshold and the median of the bootstrap thresholds were equal, the bootstrap median value should be selected as the threshold value for future studies as it is based on a series of possible samples that could be obtained from the same species and not just one static group of individuals.

Once we selected and used the optimal threshold value to classify all otters as parous or nulliparous, we calculated aAFR from data contained in the teeth alone. Because the selected threshold was robust and errors spread across the age classes, it was not surprising that the resulting  $aAFR_{\text{teeth}}$  did not differ from that calculated from reproductive tracts ( $aAFR_{\text{tracts}}$ ). Because the aAFR calculation is sensitive to small changes in the number of parous females in each age class when sample sizes are small, our finding of no difference between techniques despite sample size concerns is another indication that the cementum technique is robust.

Still, researchers should carefully consider sample size and age distributions before applying this technique.

## MANAGEMENT IMPLICATIONS

The value of monitoring changes in aAFR in long-lived mammals as a tool to understand population dynamics and health has long been recognized (Eberhardt and Siniff 1977). We demonstrated that premolar cementum light bands can be used to estimate aAFR in sea otters. Cementum analysis is nondestructive and cost-effective, and because measurements can be made on the same slide section that is used for age analysis, it allows researchers to determine aAFR from archived samples. Therefore, this approach may provide researchers and wildlife managers with an effective tool to monitor changes in aAFR in a wide variety of wildlife species. Cementum measurements may now provide researchers with the means to do so in sea otters and other wild mammals where reproductive tracts or other methods are unavailable. Application of this technique to study the phenotypic plasticity in the aAFR of northern sea otters from declining and stable populations will be presented in a separate article (also see von Biela 2007).

## ACKNOWLEDGMENTS

Our research was supported by the National Oceanic and Atmospheric Administration and North Pacific Universities Marine Mammal Research Consortium. Our study would not have been possible without samples collected by USGS, USFWS, the Alaska Stranding Network, or subsistence hunters working with The Alaska Sea Otter and Steller Sea Lion Commission. We would also like to thank J. Bodkin, J. Haddix, D. Janski, J. Haas, D. Pfeiffer, and J. Prewitt for assistance with sample collection and manuscript review. G. Matson and an anonymous reviewer greatly improved this manuscript.

## LITERATURE CITED

- Baker, J., and P. Boveng. 1997. Survey of growth layers in harbor seal teeth. Pages 107–111 in J. Baker, P. R. Becker, P. Boveng, K. Frost, S. Iverson, L. A. Jemison, B. Kelly, J. P. Lewis, L. F. Lowry, E. A. Mathews, G. O'Corry-Crowe, R. Papa, G. W. Pendleton, K. W. Pitcher, G. Sheffield, R. Small, U. Swain, R. L. Westlake, K. Wynne, and R. Zarnke. Harbor seal investigations in Alaska annual report. NOAA grant NA57FX0367. Alaska Department of Fish and Game, Division of Wildlife Conservation, Anchorage, USA.
- Bengtson, J. L., and R. M. Laws. 1985. Trends in crabeater seal age at maturity: an insight into Antarctic marine interactions. Pages 669–675 in W. R. Siegfried, P. R. Condy, and R. M. Laws, editors. Antarctic nutrient cycles and food webs. Springer Verlag, Berlin, Germany.
- Bengtson, J. L., and D. B. Siniff. 1981. Reproductive aspects of female crabeater seals (*Lobodon carcinophagus*) along the Antarctic Peninsula. Canadian Journal of Zoology 59:92–102.
- Bodkin, J. L., J. Ames, R. J. Jameson, A. M. Johnson, and G. M. Matson. 1997. Estimating age of sea otters with cementum layers in the first premolar. Journal of Wildlife Management 61:967–973.
- Bodkin, J. L., D. M. Mulcahy, and C. J. Lensink. 1993. Age specific reproduction in female sea otters (*Enhydra lutris*) from south-central Alaska: analysis of reproductive tracts. Canadian Journal of Zoology 71: 1811–1815.
- Boness, D. J., and H. James. 1979. Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. Journal of Zoology London 188:477–500.
- Choquet, D. 1991. Density-dependent growth, body condition and demography in feral donkeys: testing the food hypothesis. Ecology 72: 805–813.
- Clutton-Brock, T. H., editor. 1988. Reproductive success: studies of individual variations in contrasting breeding systems. The University of Chicago Press, Chicago, Illinois, USA.
- Coy, P. L., and D. L. Garshelis. 1992. Reconstructing reproductive histories of black bears from the incremental layering in dental cementum. Canadian Journal of Zoology 70:2150–2160.
- Craighead, J. J., F. C. Craighead, and H. E. McCutchen. 1970. Age determination of grizzly bears from fourth premolar tooth sections. Journal of Wildlife Management 34:353–363.
- DeMaster, D. P. 1978. Calculation of the average age of sexual maturity in marine mammals. Journal of the Fisheries Research Board of Canada 35: 912–915.
- Dzikowski, R., G. Hulata, S. Harpaz, and I. Karplus. 2004. Inducible reproductive plasticity of the guppy *Poecilia reticulata* in response to predation cues. Journal of Experimental Zoology 301A:776–782.
- Eberhardt, L. L., and D. B. Siniff. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34:183–190.
- Efron, B. 1982. The jackknife, the bootstrap and other resampling plans. The Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania, USA.
- Festa-Bianchet, M., J. T. Jorgenson, M. Lucherini, and W. D. Wishart. 1995. Life history consequences of variation in age of primiparity in bighorn ewes. Ecology 76:871–881.
- Francis, R. I. C. C. 1990. Back-calculation of fish length: a critical review. Journal of Fish Biology 36:883–902.
- Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. Dover, New York, New York, USA.
- Klevezal, G. A. 1996. Recording structures of mammals: determination of age and reconstruction of life history. A. A. Balkema, Rotterdam, Netherlands.
- Klevezal, G. A., and S. E. Kleinenberg. 1969. Age determination of mammals from annual layers in teeth and bones. IPST Press, Jerusalem, Israel.
- Klevezal, G. A., and A. C. J. Myrick. 1984. Marks in tooth dentine of female dolphins (genus *Stenella*) as indicators of parturition. Journal of Mammalogy 65:103–110.
- Klevezal, G. A., and B. S. Stewart. 1994. Patterns and calibration of layering in tooth of cementum of female northern elephant seals, *Mirounga angustirostris*. Journal of Mammalogy 75:483–487.
- Le Boeuf, B. J., and J. Reiter. 1991. Biological effects associated with El Niño, southern oscillation 1982–1983, on northern elephant seals breeding at Ano Nuevo, California. Pages 206–218 in F. Trillmich and K. A. Ono, editors. Pinnipeds and El Niño. Springer-Verlag, Berlin, Germany.
- McMahon, C. R., H. R. Burton, and M. N. Bester. 2003. A demographic comparison of two southern elephant seal populations. Journal of Animal Ecology 72:61–74.
- Monson, D. H., J. A. Estes, J. L. Bodkin, and D. B. Siniff. 2000. Life history plasticity and population regulation in sea otters. Oikos 90:457–468.
- Pistorius, P. A., M. N. Bester, S. P. Kirkman, and F. E. Taylor. 2001. Temporal changes in fecundity and age at sexual maturity of southern elephant seals at Marion Island. Polar Biology 24:343–348.
- Sinha, A. A., C. H. Conaway, and K. W. Kenyon. 1966. Reproduction in the female sea otter. Journal of Wildlife Management 30:121–130.
- Siniff, D. B., and K. Ralls. 1991. Reproduction, survival and tag loss in California sea otters. Marine Mammal Science 7:211–229.
- Skogland, T. 1985. The effects of density-dependent resource limitation on the demography of wild reindeer. Journal of Animal Ecology 54:359–374.
- Soderberg, S. 1978. Falling age at sexual maturity in the Baltic seals. Finnish Game and Fish Research Institute 37:27–31.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. Quarterly Review of Biology 51:3–47.
- Stewart, R. E. A., B. E. Stewart, I. Stirling, and E. Street. 1996. Counts of growth layers groups in cementum and dentine in ringed seals (*Phoca hispida*). Marine Mammal Science 12:383–401.

- Stirling, I. 2005. Reproductive rate of ringed seals and survival of pups in Northwestern Hudson Bay, Canada, 1991–2000. *Polar Biology* 28:381–387.
- Testa, J. W., D. B. Siniff, J. P. Croxall, and H. R. Burton. 1990. A comparison of reproductive parameters among three populations of Weddell seals (*Leptonychotes weddellii*). *Journal of Animal Ecology* 59: 1165–1175.
- von Biela, V. R. 2007. Evaluating and comparing reproductive parameters of northern sea otters (*Enhydra lutris kenyoni*) in Alaska. Thesis, University of Alaska Anchorage, Anchorage, USA.
- Wilson, D. E., M. A. Bogan, R. L. Brownell, Jr., A. M. Burdin, and M. K. Maminov. 1991. Geographic variation in sea otters, *Enhydra lutris*. *Journal of Mammalogy* 72:22–36.

*Associate Editor: Green.*