# PHENOTYPIC PLASTICITY IN AGE AT FIRST REPRODUCTION OF FEMALE NORTHERN SEA OTTERS (*ENHYDRA LUTRIS KENYONI*)

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Life-history theory predicts that within a species, reproduction and survival rates will differ among populations that differ in resource availability or predation rates through phenotypic plasticity. When populations are near carrying capacity (K) or when they are declining due to reduced prey resources, the average age at 1st reproduction (average AFR) is predicted to be older than in populations below K. Differences between the trajectories of northern sea otter (*Enhydra lutris kenyoni*) populations in Alaska provides an opportunity to examine phenotypic plasticity. Using premolar teeth or reproductive tracts, we estimated average AFR from demographically distinct populations of sea otters in Alaska. We obtained samples from 2 populations near K, Prince William Sound (PWS) and the Aleutian Archipelago (archived samples), and from 2 populations below K, the Kodiak Archipelago and Sitka. The average AFR was lower in populations below K (3.60 years ± 0.16 $SD$) compared to those near K (4.21 ± 0.13 years, $P < 0.001$), and differed among all populations, with the Aleutian population possessing the oldest average AFR (4.29 ± 0.09 years) followed by PWS (4.05 ± 0.24 years), Sitka (3.80 ± 0.21 years), and Kodiak (3.19 ± 0.37 years). The difference in average AFR among populations supports life-history theory and provides evidence of phenotypic plasticity in sea otters. Our findings highlight the value of using average AFR as a tool for monitoring mammalian populations.

Key words:    age at 1st reproduction, Alaska, demography, *Enhydra lutris*, life history, phenotypic plasticity, reproduction, sea otter

In an effort to maximize fitness, individuals respond to changes in the environment such as climatic conditions, food availability, and predation by allocating energy between somatic growth and maintenance, and reproduction (Clutton-Brock et al. 1983; Messier and Crête 1985; Reiter et al. 1981; Sinclair et al. 2006). At the population level, individual trade-offs are collectively manifested as demographic shifts. To understand the status of any given mammal population, the major demographic parameters needed are estimates of adult survivorship, juvenile survivorship, reproductive rate, and age at 1st reproduction (AFR—Fowler 1988). Demographic shifts may occur through 2 mechanisms: evolutionary changes in gene frequencies over many generations (Stearns 2000) or phenotypic plasticity, which reflects change across the lifetime of an individual (Clutton-Brock 1988). Phenotypic plasticity is more limited in scope than evolutionary change due to constraints imposed by the physiological capacity of the species. From a conservation perspective, phenotypic plasticity in demographic rates is of particular interest because response to environmental conditions will generally occur at rates faster than evolutionary changes in long-lived species. Phenotypically plastic changes in demographic rates can occur within an individual's lifetime, and may partially or completely compensate for environmental change that can affect fitness.

The population density of a long-lived mammal will fluctuate in response to resource availability within its habitat. When the population growth rate for mammals is increasing, either in response to colonizing new habitat or an influx of new prey resources, survival of adults and juveniles and reproductive rates all tend to increase, whereas AFR decreases (Boutin 1990; Choquenot 1991). However, as resources become limited and the population approaches the environ-

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mental carrying capacity (K), survival and reproductive rates start to decrease, and AFR increases. Within a population, changes in demographic parameters typically occur in a staggered fashion that will likely maximize lifetime reproductive output (Eberhardt 2002). Juvenile survival is often considered the 1st parameter to decline, followed by an increase in AFR, a decrease in reproductive rates, and finally decreases in adult survival (Clutton-Brock et al. 1983; Fowler 1981; Gaillard et al. 1998). Decreases in reproductive output as populations reach K and become food limited reflect a shift in energy partitioning from reproduction to somatic growth and maintenance in an effort to maintain survival (Boutin 1990; Stearns 1976). Taken together, decreases in reproductive output and survival slow population growth and can lead to either population stability or decline.

When a population declines in density, shifts in the demographic parameters can be informative as to the cause of the decline. If a population decline is precipitated by bottom-up sources (limitations in resource availability), changes in life-history parameters mirror those that occur as a population reaches K (Fowler 1981; Gaillard et al. 1998). Therefore, bottom-up declines are associated with increases in AFR and reductions in reproductive and survival rates (Pistorius et al. 2001). In contrast, top-down population declines reduce the survival of 1 or more age classes by direct mortality, such as increased predation or exploitation rates, and the lowered population densities typically reduce competition for food resources, allowing surviving individuals to grow to adult body size more quickly and allocate more energy to reproductive output (Stearns 1976). As a result, top-down declines are often associated with increases in reproductive rate and younger AFR (Boyce 1981; Dzikowski et al. 2004). Although these patterns have broad support in mammals, there are exceptions, including deviations from these patterns that arise from the sublethal impacts of predators on prey that may alter reproductive output through changes in behavior (Creel et al. 2007; Wirsing et al. 2008). Because changes in AFR differ depending on the cause of population decline and are detectable, whereas survival rates decline regardless of the cause and are usually difficult to detect, examining changes in AFR could be more informative than changes in survival rates.

In Alaska, the natural history of northern sea otters (*Enhydra lutris kenyoni*) provides a unique perspective for understanding the relationship between AFR relative to K because samples are available from numerous demographically distinct populations (Fig. 1; Angliss and Lodge 2004; Gorbics and Bodkin 2001). Populations of sea otters at many islands in the Aleutian Archipelago were likely to be near K during the 1960s and 1970s when a large sample of reproductive tracts was obtained (Kenyon 1969; Schneider 1975). Samples are available from another population of sea otters in southwestern Alaska also thought to be below K, the Kodiak Archipelago. The sea otter population at Kodiak increased from a remnant group following the cessation of hunting in 1911 until the 1990s (Bodkin et al. 1999). The population trend appears less certain now, but unoccupied



FIG. 1.—Locations of samples of sea otters (*Enhydra lutris kenyoni*) used in this study delineated by region. The areas are indicated by shapes corresponding to the population status: circles indicate where samples were collected from populations near carrying capacity (K) and triangles indicate where samples were collected from populations below K.

habitat with abundant food resources available along the southern end of the archipelago supports the assumption that this population is still below K. Within south-central Alaska, samples were collected in Prince William Sound (PWS), a near-K population as indicated by the stable trend in surveys of abundance (Bodkin et al. 2002), and in a population along the northern Kenai Peninsula thought to be below K, as supported by available habitat but relatively little population survey data (Angliss and Lodge 2004). Lastly, collections have been made in southeastern Alaska where sea otters were reintroduced during the mid-1960s and populations have generally been increasing rapidly into abundant unoccupied nearshore habitat (Bodkin et al. 1999, 2004, 2007; Esslinger and Bodkin 2009). All populations in southeastern Alaska are thought to be below K, but the reintroduction location near Sitka may be closer to K than other areas. Determining the relative K of a population, or how close a population is to its K, can be a difficult task due to error associated with population surveys and uncertainty in carrying capacity. Because of this difficulty, populations were only classified in 2 broad categories, near K or below K.

Because of the widespread distribution of sea otters in Alaska and the differences between long-term population trajectories, it is not surprising that baseline or current values for demographic parameters like AFR are not known for most populations. We employed a new technique to estimate average AFR of females that allows researchers to use archived premolar teeth of sea otters, routinely collected across Alaska for age determination (von Biela et al. 2008). With this method it was possible to obtain estimates of average AFR in populations throughout the sea otter's range in Alaska during 1993–2006, and make comparisons to the historic collection from the Aleutian Archipelago (1967–1971). The goal of our study was to

TABLE 1.—Source of reproductive tracts or premolar teeth of sea otters (*Enhydra lutris kenyoni*) used for determination of average age at 1st reproduction (average AFR). Samples came from the Aleutian Archipelago (Adak, Amchitka, Tanaga, Kanaga, and Deraolf islands) and Kodiak Archipelago (Kodiak and Afognak) in southwestern Alaska, Prince William Sound and the Kenai Peninsula (Kachemak and Resurrection bays) in south-central Alaska, and the areas near Sitka (Baranof, Chichagof, and Kuiu islands), Yakutat, and Ketchikan (Prince of Wales Island) in southeastern Alaska. Sources are abbreviated as follows: Alaska Department of Fish and Game (ADF&G), United States Fish and Wildlife Service (USFWS), and the Alaska Sea Otter and Steller Sea Lion Commission (TASSC). Carrying capacity is abbreviated as K and the population status is classified as either near or below K. An individual sample may have been used in both analyses. Different letters indicate significant difference between average AFR ($P < 0.05$).

| Years, region, and population sampled | Source | Relative K | AFR $n$ (harvest; stranded) | AFR $\pm$ SD |
|---|---|---|---|---|
| 1967–1971 | | | | |
|   Southwestern Alaska | | | | |
|     Aleutian Archipelago | ADF&G | Near | 692; 0 | 4.29 ± 0.09[a] |
| 1993–2006 | | | | |
|   Southwestern Alaska | | | | |
|     Aleutian Archipelago | TASSC and USFWS | Below | 4; 0 | — |
|     Kodiak Archipelago | TASSC and USFWS | Below | 48; 2 | 3.19 ± 0.37[b] |
|   South-central Alaska | | | | |
|     Prince William Sound | TASSC and USFWS | Near | 86; 1 | 4.05 ± 0.24[c] |
|     Kenai Peninsula | TACCS and USFWS | Below | 7; 8 | — |
|   Southeastern Alaska | | | | |
|     Sitka | TASSC and USFWS | Below | 85; 1 | 3.80 ± 0.21[d] |
|     Ketchikan | TASSC and USFWS | Below | 22; 0 | — |
|     Yakutat | TASSC and USFWS | Below | 8; 0 | — |
| Total | | | 964 | |

examine these materials for evidence of reproductive phenotypic plasticity among otter populations.

## MATERIALS AND METHODS

Reproductive tracts or premolar teeth, or both, were collected from 1,462 female sea otters over 2 time periods, and from multiple populations (Table 1; Fig. 1). In the Aleutian Archipelago population, 1,155 otters were collected through experimental harvests in the Rat and Delarof island groups (Adak, Amchitka, Kanaga, Tanaga, and Delarof islands) between May and October of 1967–1971 by the Alaska Department of Fish and Game. These samples were originally analyzed for signs of past and current reproduction by Schneider (1975). An additional 306 samples collected between 1993 and 2006 came from otters sampled in the Aleutian Archipelago (Adak and Unimak islands; $n = 7$) and Kodiak Archipelago (Kodiak and Afognak Islands; $n = 55$) in southwestern Alaska, PWS ($n = 94$), the Kenai Peninsula (Kachemak and Resurrection bays; $n = 31$) in south-central Alaska, and the areas around Sitka (Baranof, Chichagof, and Kuiu islands; $n = 89$), Yakutat ($n = 8$), and Ketchikan (Prince of Wales Island; $n = 22$) in southeastern Alaska. United States Fish and Wildlife Service and the Alaska Sea Otter and Steller Sea Lion Commission provided all samples collected after 1993 primarily through subsistence hunting, which occurs throughout the year, but also with a few stranded animals (Table 1). In each sample set a bias against females with pups exists, supporting the assumption that the 2 collections are comparable (Schneider 1975).

The age of each otter in this study was determined by counting cementum annuli in premolar teeth as described in Bodkin et al. (1997). The cementum annuli are dark narrow layers separated by wide transparent layers or light bands that are laid down around the outside of the tooth within the gums at a rate of 1 annulus per year (Klevezal 1996). Premolar teeth were decalcified, sectioned longitudinally, and stained with Giemsa solution. Teeth from the Aleutians (1967–1971) were prepared and analyzed by K. Schneider (Alaska Department of Fish and Game, Anchorage, Alaska), and all other samples were prepared and analyzed by Matson's Laboratory, LLC (Milltown, Montana). For those samples processed by Matson's Laboratory, only premolars with an age certainty code of A or B (possible error judged to be $\pm 0$ years and $\pm 1$ year, respectively, for otters 0–7 years—G. Matson, pers. comm.) were used in this study to minimize error. Unfortunately, direct comparison between techniques could not be performed because the slides previously aged by Schneider had so degraded over time that they could not be accurately analyzed by Matson's Laboratory.

The average AFR was determined by classifying each otter as parous or nulliparous, and then by using the parous status to estimate average AFR following DeMaster (1978). Individuals were classified as parous or nulliparous based on either analysis of reproductive tracts (Aleutians 1967–1971) or width measurements of cementum light bands (1993–2006 time period). Otters collected in the Aleutian Archipelago in 1967–1971 were classified as parous if either a corpus luteum or corpus albicans was present in the reproductive tract. The presence of a corpus luteum is indicative of current pregnancy, but a corpus albicans is indicative of past pregnancy, because the corpus luteum becomes a corpus albicans. For the purpose of this study all females with a corpus luteum or corpus albicans were considered parous. The method of classification

removes the potential bias of seasonal differences in the timing of collection relative to the peak pupping season, because primiparous females sampled early or late in the year would both be considered parous (due to presence of a corpus luteum or corpus albicans, respectively).

In the samples collected from 1993 to 2006, individual females were classified as parous or nulliparous based on the narrowing of cementum light bands. Declines in premolar cementum have been linked to the onset of reproduction in a variety of species including seals and bears (Bengtson and Siniff 1981; Coy and Garshelis 1992; Klevezal 1996; Klevezal and Stewart 1994; Soderberg 1978). In fact, for black bears (*Ursus americanus*), individual cub-rearing years can be identified in cementum bands (Coy and Garshelis 1992). In our previous validation of this technique for sea otters, the width of each premolar light band was measured and standardized to the widest light band at each of 3 measurement sites (von Biela et al. 2008). Then, the average standardized measurement was determined for each complete year of the otter's life. Restricting the analysis to complete years was necessary because the last light band was not complete and could not be measured, but also has the benefit of avoiding issues with seasonality. If the narrowest cementum light band measurement was ≤0.32 the width of the widest light band, the otter was classified as parous in the last complete year, which is to say at age x − 1. This threshold was determined empirically by directly comparing parous status determined from 92 paired premolar and reproductive tracts. Because there was close agreement between the techniques (83% of female otters properly classified as parous), no indication of bias (similar percentages were misclassified as parous when not, and nulliparous when parous), and because bootstrap replicates ($n = 1,000$) of the threshold value indicated that the threshold was robust, this same technique and threshold value were used to determine the parous status of female otters (1993–2006) in this study.

At the population level, we have previously demonstrated that the reproductive tract and cementum width techniques do not produce statistically different estimates of average AFR (von Biela 2007; von Biela et al. 2008). In both cases, average AFR was estimated following DeMaster's (1978) equation. The average AFR was calculated as follows:

$$AFR = \sum_{x=1}^{w} xP(x)$$

and

$$P(x) = f(x) - f(x-1),$$

where x is age, $f(x)$ is the proportions of females in an age class displaying evidence of past reproduction, and w is the oldest age in the sample of the age when all females in the sample are reproductive. The estimated variance for average AFR is:

$$v(AFR) = \sum_{x=1}^{w-1} \frac{f(x)[1-f(x)]}{n_x - 1} + \frac{w^2 f(w)[1-f(w)]}{n(w)-1},$$

where x, $f(x)$, and w are as above and $n$ is sample size.

The calculation of average AFR uses sample sizes in each age class to calculate the variance of $f(x)$ for the age class. Although otters do not reproduce during their 1st year of life, their inclusion in the calculation improves the average AFR estimate and reduces the variance. The age distribution of the sample does not need to be representative of the age distribution of the population because the equation uses only the age-specific proportion of parous females (e.g., the proportion of age 2 samples does not matter, but the number of age 2 samples used to calculate the $P(x)$ is important to variance). However, absolute sample size is important. DeMaster (1978) noted that ~25 individuals per indeterminate age class (age classes with $0 < f(x) < 1$) were necessary to detect a difference of one-half year when he assumed maximum variance. In general, sample sizes in the Aleutians (1967–1971) were well above this guideline, PWS and Sitka were near the guideline, and sample sizes from Kodiak were somewhat below the guidelines (~10 samples per age). In each case, the sample size is reflected in the variance of an average AFR estimate and may impact comparisons among populations by increasing the detection limit. However, this reduced statistical power is only a concern if significant differences are not detected among populations. Any difference detected among populations would be genuine.

The average AFRs were compared among populations and by population status (below versus near K). The average AFRs for otters were compared among Aleutian 1967–1971, Kodiak, PWS, and Sitka 1993–2006 populations using an analysis of variance (ANOVA) for summary statistics that accounts for the multiple comparisons (Larson 1992). Differences in average AFR between otters below K (Kodiak, Aleutians, Kenai, Sitka, Yakutat, and Ketchikan 1993–2006) and otters near K (Aleutians 1967–1971 and PWS 1993–2006) were tested using a *t*-test. An average AFR for otters from the Aleutian Archipelago, Kenai Peninsula, Ketchikan, and Yakutat populations 1993–2006 could not be calculated because of low sample sizes from these populations. However, all individuals were sorted into below- or near-K categories and included in the comparison of populations by status.

## RESULTS

The average AFR differed significantly in all population comparisons for the 1993–2006 otters (all possible pairwise comparisons, ANOVA for summary statistics, $P < 0.05$; Table 1). Otters from Kodiak had the youngest average AFR (versus PWS, $t = 16.29$, $d.f. = 132$, $P < 0.001$; Sitka, $t = 12.15$, $d.f. = 131$, $P < 0.001$). PWS and Sitka had the most similar average AFRs, but were still significantly different ($t = 7.25$, $d.f. = 169$, $P < 0.001$). The average AFR of otters in the Aleutians (SW, 1967–1971) was significantly older at $4.29 \pm 0.09$ (mean $\pm SD$) years than Kodiak (3.19 years, $t = 21.55$, $d.f. = 738$, $P < 0.001$), PWS (4.05 years, $t = 18.05$, $d.f. = 776$, $P < 0.001$), or Sitka (3.80 years, $t = 38.92$, $d.f. = 775$, $P < 0.001$). Differences in average AFR were driven primarily though changes in the proportion of parous 2- and 3-year-old females (Fig. 2).
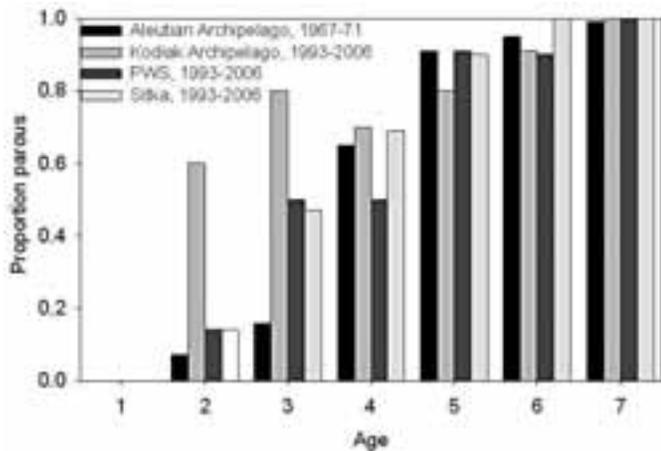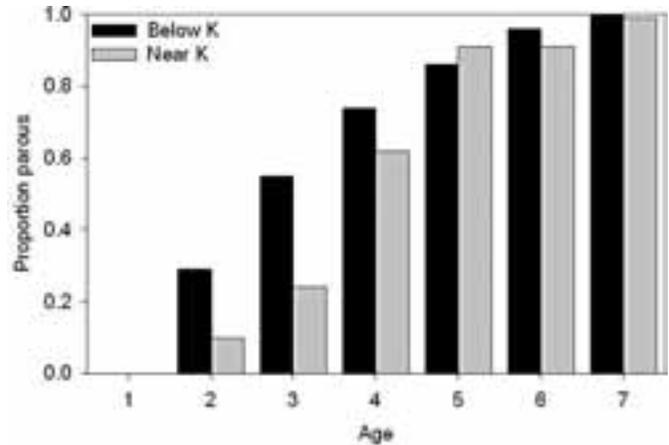
FIG. 2.—The proportion of parous female sea otters (*Enhydra lutris kenyoni*) of ages 1–7 years used to calculate the average age at 1st reproduction (average AFR) for the Aleutian Archipelago, Kodiak Archipelago, Prince William Sound (PWS), and Sitka, Alaska, populations of sea otters.

Similarly, the average AFR of female otters from all populations below K was significantly younger than that of female otters from all populations near K (3.60 ± 0.16 versus 4.21 ± 0.13 years, $t = 54.73$, $d.f. = 961$, $P < 0.001$), which was the result of an increase in the proportion of parous 2- and 3-year-olds just as in the population comparison (Fig. 3).

## DISCUSSION

The pattern of difference in average AFR among sea otter populations fits with predictions from life-history theory that average AFR would be higher in stable populations presumably near K, and lower in those below K. Differences in average AFR between populations were <1 year and fell within 3 and 5 years of age, as previously reported for sea otters (Bodkin et al. 1993; Jameson and Johnson 1993; Kenyon 1969; Monson et al. 2000; Schneider 1975). Although differences in average AFR may seem small, they were consistently detected and align well with work in other mammals. For example, decreases in resource availability have been linked with increases in AFR of approximately 1 year in both southern elephant seals (*Mirounga leonina*—McMahon et al. 2003) and red deer (*Cervus elaphus*—Langvatn et al. 1996), whereas increased harvest pressure, and the associated decrease in population density, have been linked with a 1-year decline in AFR for beavers (*Castor canadensis*) in Alaska (Boyce 1981).

The 2 stable populations near K, PWS 1993–2006 and Aleutian 1967–1971 (Bodkin et al. 2002; Kenyon 1969) had the highest average AFRs at just above 4 years. A similar AFR also was noted in otters collected as a result of the 1989 *Exxon Valdez* oil spill (Bodkin et al. 1993), a further suggestion that the PWS population is and has been near K. In contrast, the sea otter populations across southeastern Alaska are likely below K, because they were reestablished by translocations of a small number of otters from the Aleutian Archipelago and



FIG. 3.—The proportion of parous female sea otters (*Enhydra lutris kenyoni*) of ages 1–7 years used to calculate the average age at 1st reproduction (average AFR) for populations of sea otters below carrying capacity (K; Kodiak, Aleutians, Sitka, Yakutat, and Ketchikan 1993–2006) or near K (Aleutians 1967–1971 and Prince William Sound 1993–2006).

PWS in the 1960s and 1970s (Jameson et al. 1982). Given that the availability of food resources in this area is likely higher than in PWS because of differences in relative K (Bodkin et al. 2002, 2004), it is not surprising that average AFR was younger in Sitka than in PWS, Alaska.

The average AFR of sea otters from the below-K population in the Kodiak Archipelago (Monson et al. 2000) is much younger than either PWS or Sitka, Alaska, populations. The younger average AFR in the Kodiak Archipelago population suggests that resource availability was not limiting population abundance at the time of sampling. Because the recent population surveys in Kodiak have shown large uncertainty, it has been difficult to determine the approximate rate of population change; this kind of demographic information is helpful to managers who are tasked with maintaining abundance of sea otters across Alaska.

When otters from all areas in Alaska were compared by the hypothesized relative K (below K versus near K; Fig. 3), the younger average AFR for the below-K group was consistent with expectations from life-history theory. The categories of below and near K certainly encompass a wide variety of conditions. Otters in the below-K group came from populations that are currently thought to be declining, increasing, well below K, and approaching K. In the near-K group, otters were combined from Aleutian Archipelago and PWS even though methods of analysis differed and the PWS otters were greatly outnumbered (only 13% of the samples). However, the independent estimates of average AFR were above 4 years for each of these groups. The difference between average AFR by relative K indicates that otters from below-K populations do employ a similar life-history strategy with regard to AFR as postulated by life-history theory despite potential differences in population trajectory. Furthermore, the difference in average AFR based upon relative K would not be anticipated if AFR was primarily genetically determined. Instead, AFR is likely to be a phenotypically plastic trait. Given the history of translocations

for these otter populations and generation time in sea otters, it also seems unlikely that enough time would have passed to allow genetic differentiation in average AFR. Together, the results suggest that the AFR is related to the relative carrying capacity as anticipated based on life-history theory.

Our results cannot be used to address the question of whether the ongoing population decline in the Aleutian Archipelago is caused by top-down predation because there are not enough recent samples available to derive a current estimate of average AFR. However, Aleutian otters have recently been shown to grow faster and be in better condition than otters taken in 1967–1971 (same samples used in this study—Laidre et al. 2006). Because increases in individual growth rates are often correlated with decreases in AFR (Laws 1956), these faster growth rates, in combination with the observed variation in average AFR across the sea otter's range, suggest that the current average AFR in the Aleutian otter population is younger than it was over the 1967–1971 period. Similar changes in average AFR have been observed in beavers undergoing increased mortality due to exploitation (Boyce 1981).

Few data on AFR exist for sea otter populations outside of Alaska. The proposed link between population status and average AFR would indicate that those populations below K would have younger AFR, whereas populations near K would have older average AFR. Because populations of sea otters in Washington and British Columbia, Canada, have rates of growth near the maximum rate of increase, a younger average AFR of ~3 years would be anticipated (Bodkin et al. 1999; Estes 1990). In contrast, the population of California sea otters has maintained slow growth for many decades, making it more likely that average AFR is older (4 years or above—Bodkin et al. 1999; Estes 1990). Results of Jameson and Johnson (1993) for the California sea otter concur with the assumption of older AFR by documenting that 6 of the 9 known females had their 1st pup at age 4 or above.

The findings in our study fit with independently supported classifications of population status, but there are potential sources of bias and error in comparing populations. These include biases in estimates of animal ages, bias in collection of samples, and error in classification of parous status. Biases in otter ages are most likely in the comparisons with the Aleutian 1967–1971 populations because age of otters was estimated by different readers than samples from the other populations and time periods. However, this bias should be small because Schneider's (1973) technique (used on all samples collected between 1967 and 1971) was the basis of the protocols used by Matson's Laboratory to estimate age of otters from 1993 to 2006 (G. Matson, pers. comm.), and research examining among-reader error in estimating ages from cementum in teeth of sea otters revealed some error, but little evidence of observer bias (Bodkin et al. 1997). A 2nd potential source of bias could have been introduced due to collection methods, particularly if hunters avoided collecting females with pups (Eberhardt and Schneider 1994; Schneider 1975), or if stranded animals were of a particular age class. Although otters during 1 small part of the collections from the 1967–

1971 Aleutian samples were taken in a random fashion, Schneider's (1975) report indicates that in the vast majority of collections hunters avoided females with pups. Recent accounts echo similar hunting practices by subsistence users. Thus, there was no indication that these biases changed across time or regions, nor was any particular age class represented in the stranded animals used in this study. Therefore, it is unlikely that results were biased in a way that would make comparisons among populations invalid.

Systematic errors could have been introduced into the average AFR calculations if parous status was not accurately determined due to errors made when examining reproductive tracts, measuring cementum annuli, or setting the threshold cementum width (see von Biela [2007] or von Biela et al. [2008] for a discussion of potential errors). Temporal differences in average AFR could originate if the methods produced consistently different estimates of parous status, but our previous validation study failed to find a significant difference between techniques (von Biela 2007; von Biela et al. 2008), suggesting that temporal differences are real. Spatial differences in average AFR among populations within the recent sample cannot be attributed to methodological differences in estimating age or hunting techniques or parous classification, and support the conclusion that average AFR is a phenotypically plastic trait. Although the focus of our study has been comparisons of average AFR among populations, it also is important to acknowledge the variation in AFR within a population. There is no way to determine what proportion of variance in our estimates is due to process versus measurement error. Possible sources of measurement error within populations are similar to those among populations as described above. Much of the variation within populations also could be due to process error, particularly because individuals were collected over a number of years and across multiple islands, bays, or inlets in a given region.

This study is the 1st to document evidence of phenotypic plasticity in a sea otter reproductive parameter. Previous research on reproductive plasticity in sea otters did not document phenotypic plasticity in reproduction, but reproductive rates, rather than AFR, were the focus of the investigation (Monson et al. 2000). Despite the evidence of plasticity in average AFR found here, this trait is unlikely to have a direct impact on population regulation because of its low impact on lifetime reproductive output (Eberhardt and Siniff 1977). We agree with the conclusion of Monson et al. (2000) that populations of sea otters are most likely regulated in a direct manner through changes in juvenile mortality. However, it also is important to point out that the trade-offs present between reproduction and survival could allow a female the ability to delay AFR in areas of limited resources to increase her chance of survival or her pup's chance of survival by waiting to reproduce at a time when her body condition is higher (Festa-Bianchet et al. 1995; Reiter and Le Boeuf 1991). Through consequences upon the female's survival and the survival of her offspring, changes in AFR may become more important to population regulation, as previous studies have documented for northern elephant seals (*Mirounga angustirostris*—Reiter and Le Boeuf 1991) and bighorn ewes

(*Ovis Canadensis*—Festa-Bianchet et al. 1995). Further research would be necessary to determine if plasticity in AFR led to similar survival benefits for sea otters.

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