

## Age-specific reproduction in female sea otters (*Enhydra lutris*) from south-central Alaska: analysis of reproductive tracts

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We estimated age at sexual maturity and age-specific reproductive rates by examining carcasses and reproductive tracts from 177 female sea otters (*Enhydra lutris*). Carcasses were recovered from south-central Alaska, primarily from western Prince William Sound, as a result of the T/V *Exxon Valdez* oil spill in 1989. We found 65% of our sample to be sexually mature. Sexual maturity was first attained at age 2. The proportion of sexually mature animals increased from 30% at age 2 to 100% at age 5. Annual reproductive rates increased from 22% at age 2 to 78% at age 5 and remained relatively stable (75–88%) through to age 15. The sex ratio ( $\sigma$ : $\varphi$ ) of 49 fetal sea otters was 18:37 and differed significantly from parity. Females younger than 8 tended to produce more female fetuses, while older mothers did not. Our estimates of the reproductive characteristics of female sea otters obtained by examination of reproductive tracts were similar to those reported in the literature based on in situ observations of marked individuals.

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Nous avons estimé l'âge de la maturité sexuelle et les taux de reproduction spécifiques à chaque classe d'âge en examinant les carcasses et les systèmes génitaux de 177 femelles de Loutres de mer (*Enhydra lutris*). Les carcasses examinées ont été récupérées dans le centre sud de l'Alaska, surtout dans la partie ouest du détroit de Prince William, à la suite de la fuite de pétrole du T/V *Exxon Valdez* en 1989. Soixante-cinq pourcent des individus examinés avaient atteint leur maturité sexuelle. D'après les résultats de l'étude, les premières femelles à atteindre leur maturité sexuelle sont âgées de 2 ans. La proportion des femelles à maturité augmente en fonction de l'âge; elle est de 30% chez les femelles de 2 ans et de 100% chez les femelles de 5 ans. Les taux annuels de reproduction augmentent aussi en fonction de l'âge et sont de 22% à l'âge de 2 ans, et de 78% à l'âge de cinq ans; ils demeurent relativement stables (75–88%) jusqu'à l'âge de 15 ans. Le rapport mâles:femelles a été déterminé à l'examen de 49 fœtus, et sa valeur, 18:37, diffère significativement de la norme. Les femelles âgées de moins de 8 ans produisent plus de fœtus femelles, tendance que ne manifestent pas les femelles plus âgées. Les caractéristiques relatives à la reproduction chez les Loutres de mer femelles, telles que révélées par l'examen des tractus génitaux, sont semblables à celles qui ont été décrites dans la littérature à la suite d'observations in situ d'individus marqués.

[Traduit par la rédaction]

### Introduction

Age-specific reproductive rates are important variables in the population dynamics of long-lived mammals (Caughley 1977; Eberhardt 1985), and may respond to habitat quality and availability of resources (Bronson and Rissman 1986; Bronson 1989; Garrott et al. 1991). Reproductive rates as well as reproductive success (production of offspring that attain maturity) may vary with a female's experience (Altman et al. 1988; Le Boeuf and Reiter 1988) as well as with environmental factors (Bronson 1989). In addition, reproduction may decline with the onset of senescence (Clutton-Brock 1988; Garrott et al. 1991).

Reproductive characteristics of sea otters have been studied by visual observation of marked individuals (Loughlin et al. 1981; Payne and Jameson 1984; Wendell et al. 1984; Siniff and Ralls 1991; Jameson and Johnson 1993; Monson and DeGange<sup>2</sup>) and by analysis of reproductive tracts of dead animals (Kenyon 1969; Schneider 1973b; Sinha et al. 1966). Previous studies have been conducted at sites in Alaska and California, enabling comparisons of reproductive characteristics among populations to be made.

Following the grounding of the T/V *Exxon Valdez* in Prince William Sound in March 1989, and the subsequent oil spill, 781 sea otter carcasses were recovered from Prince William Sound, the Kenai and Alaska Peninsulas, and Kodiak Island (Doroff et al. 1993). This provided an opportunity to investigate the reproductive biology of female sea otters from south-central Alaska through the study of reproductive tracts. Our objectives in this study were to: (i) estimate age-specific reproduction in female sea otters from south-central Alaska, (ii) compare the results of reproductive studies using reproductive tracts and visual observations of live animals, and (iii) examine the assumptions associated with methods of estimating reproductive characteristics in female sea otters.

### Methods

We examined reproductive tracts from 177 female sea otters recovered during the response to the T/V *Exxon Valdez* oil spill. Only reproductive tracts where tissue quality was suitable for examination and the carcass recovery location was known were used. Animals were collected from 30 March to 30 August of 1989 in Prince William Sound, the Kenai Peninsula, Kodiak Island, and the southeastern coast of the Alaska Peninsula.

Ages of animals were estimated from decalcified longitudinal sections of premolar teeth (Garshelis 1984; Pietz et al. 1988). At least four sections were prepared and read from each tooth by Matson's Laboratories (Box 308, Milltown, Mont.). No birth date was assumed in the interpretation of the annuli, only that deposition occurred dur-

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<sup>2</sup>D. Monson and A. De Gange. Reproduction and survival of sea otters at Kodiak Island, Alaska. In preparation.

TABLE 1. Estimates of age at sexual maturity and age-specific reproductive rates of 177 female sea otters from southcentral Alaska

Age-class (years)	No. of females	Reproductive tract analysis			
		Proportion pregnant	Proportion lactating	Proportion reproductively mature <sup>a</sup>	Reproductive rate <sup>b</sup>
0	14	0.00	0.00	0.00	0.00
1	22	0.00	0.00	0.00	0.00
2	27	0.18	0.04	0.30	0.22
3	11	0.64	0.00	0.73	0.64
4	11	0.36	0.36	0.73	0.73
5	9	0.67	0.11	1.00	0.78
6-7	19	0.63	0.21	0.95	0.84
8-9	17	0.70	0.18	1.00	0.88
10-11	19	0.63	0.16	1.00	0.79
12-13	20	0.75	0.10	1.00	0.85
14-15	8	0.75	0.00	1.00	0.75

<sup>a</sup>As determined by the presence of placental scars, fetuses, unimplanted embryos, or lactation.

<sup>b</sup>As determined by the presence of a fetus, embryo, or lactation.

ing winter. To evaluate our age estimates, 29 two- and three-year-old otters (as estimated by Matson) were aged according to the development of cranial bones and suture closure as outlined by Lensink (1962). Of the 29 sea otters aged by both Matson and Lensink's methods, 23 agreed exactly. Two that Matson aged at 2 years were estimated as age 3 by Lensink's method. Four animals that Matson aged at 3 years were aged at 2 years by Lensink's method. The estimated ages obtained from each of these methods were compared using the Wilcoxon signed-rank test and were not significantly different ( $P > 0.10$ ). Therefore, calculations were based on age estimates obtained from tooth readings.

External examinations of the carcasses for lactation were made prior to freezing and weights and total lengths were recorded. Reproductive tracts were preserved in 10% formalin following removal from fresh or frozen carcasses. Uteri were opened and the length, weight, and sex of embryos and fetuses were recorded. Fetuses were classified into five weight classes (<1 g, >1 to 10 g, >10 to 100 g, >100 to 1000 g, >1000 g) (Kenyon 1969). Comparisons of mean total lengths and weights of females and fetuses were done with *t*-tests. Fetal sex ratios were compared through  $\chi^2$  analysis.

The lining of each uterine horn was examined and the number of placental scars (indicating past pregnancies) recorded. Placental scars were classified as either fully resolved or recent. Placental scars that were fully resolved and healed appeared as a disruption in the mucosal wrinkles of the luminal surface of the uterus, reflecting the attachment site of the placenta. This type of scar was considered not to be from a recent pregnancy. Scars that were in the resolving process, had an obviously roughened surface, were reddish in color, and were in a distended uterine horn, were considered evidence of parturition within the last 6 months (the mean sea otter gestation period; Wendell et al. 1984; Jameson and Johnson 1993). Recent parturition (6 months or less) was confirmed in all cases by lactation. Ovaries were removed and longitudinal sections of about 1-mm thickness were made by hand from both ovaries; both faces of each section were examined for corpora albicantia (whitish in color, scarlike in texture, with a dark central wrinkle) and corpora lutea (yellowish, soft in texture, and occasionally with a hollow center).

Females were categorized in two ways: recent reproductive status, and reproductive history. Recent reproductive status categories included: (i) pregnant-implanted (fetus or embryo present), (ii) pregnant-unimplanted (corpus luteum present but no indication of embryo or fetus), (iii) lactating (had dependent pup at or near time of death), and (iv) not pregnant. The pregnant-unimplanted category included animals with implanted but microscopic embryos and possibly animals recently in estrus but not bred or fertilized. Based on the morphologi-

cal similarity of the postfertilization uterus observed in pregnant-unimplanted and pregnant-implanted sea otters (Sinha et al. 1966) we did not consider it necessary to locate a blastocyst to confirm the classification of pregnant-unimplanted. Recent reproductive status was used to estimate annual reproductive rates, calculated by dividing the number of females in an age-class by the number that had or would have produced a pup between 1 October 1988 and 30 September 1989. Annual reproductive rate calculations assume a 12-month reproductive interval.

Reproductive history categories included: (i) nulliparous (not pregnant and no placental scars or ovarian structures), (ii) primiparous (presence of a single placental scar, embryo, fetus, or lactation), or (iii) multiparous (presence of more than one scar, or a scar and embryo or fetus). Reproductive history and recent reproductive status were used in combination to estimate the proportion of females that were reproductively mature (defined by past or present reproductive events) in each age class. Females  $\geq 6$  years of age were grouped into 2-year age-classes.

## Results

Of the 177 female carcasses we examined, 149 (85%) were recovered from western Prince William Sound, 15 (8%) from the Kenai Peninsula, 11 (6%) from Kodiak Island, and 2 (1%) from the Alaska Peninsula. Most carcasses we examined (135 of 177; 76%) were recovered during the first 30 days following the spill. A total of 115 (65%) of the 177 were sexually mature. Of these, 64 (56%) were pregnant-implanted, 15 (13%) were pregnant-unimplanted, 18 (16%) were lactating, and 18 (16%) were not pregnant. The remaining 62 females (35%) were considered immature. The mean total length ( $\pm 1$  standard deviation) of mature females aged 2, 3 or 4 was 48.9 cm ( $\pm 2.92$ ,  $N = 22$ ) and was significantly greater ( $P < 0.01$ ) than the mean length of immature females of the same age ( $45.4 \pm 2.5$  cm,  $N = 21$ ).

The proportion of females that were reproductively mature increased from 30% at age 2 (in their third year of life) to 73% at age 3. All animals (except one) aged 5 or older were considered mature (Table 1). The annual reproductive rate increased from 22% at age 2 to 88% for ages 8 and 9 and varied slightly for animals older than 9 (Table 1). In 97 of the 115 (84%) otters we considered reproductively mature, sexual maturity was verified by pregnancy or lactation; placental scars indi-

cated maturity in the remainder. All lactating females had a placental scar. The reproductive rates for all females  $\geq$  age 3,  $\geq$  age four, and  $\geq$  age 5 years old, and finally, for all sexually mature females were 80% ( $N = 91$ ), 82% ( $N = 84$ ), 83% ( $N = 76$ ) and 84% ( $N = 115$ ), respectively. The reproductive rate of the oldest age-class of females (14–15 years) declined to 75%; however, only eight females were represented in this age-class.

Placental scars were first observed in 2-year-old female sea otters (Fig. 1). The mean number of placental scars observed in each pair of uterine horns increased from 0.17 ( $\pm 0.39$ ,  $N = 27$ ) at age 2, 0.50 at age 3 ( $\pm 0.76$ ,  $N = 8$ ), 0.57 ( $\pm 0.53$ ,  $N = 7$ ) at age 4 and averaged 1.2 ( $\pm 0.96$ ,  $N = 58$ ) for all older age-classes with the exception of age 9 when the mean was 0.78 ( $\pm 0.67$ ,  $N = 9$ ). A maximum of five placental scars were observed in one 8-year-old animal.

Ovarian structures (corpora lutea and corpora albicantia) were observed in two of 19 one-year-old females (Fig. 1). The mean number of ovarian structures generally increased from 0.11 ( $\pm 0.31$ ) at age 1 to 3.12 ( $\pm 2.59$ ,  $N = 8$ ) at age 5 then fluctuated from 1.7 ( $\pm 0.63$ ,  $N = 13$ ) at age 6 to 6.0 ( $\pm 2.0$ ,  $N = 3$ ) at age 15. A maximum of nine ovarian structures were observed in two females, aged 8 and 14 years.

Forty-nine fetuses were recovered from pregnant otters. The sex ratio ( $\sigma:\varphi$ ) of these 49 fetuses was 17:32 (1:1.9), which differed significantly from parity ( $P < 0.05$ ;  $\chi^2$  test). We detected no significant difference ( $P > 0.1$ ) in the sex ratio of fetuses produced by young females (age  $\leq 7$ ) compared with older females (age  $\geq 8$ ), although a trend toward younger females producing female offspring and older females producing male offspring was apparent. The sex ratio of 27 fetuses of females age 7 or younger was 7:20 while the sex ratio of 22 fetuses of females age 8 and older was 10:12. The number of fetuses in each size class was as follows:  $< 1$  g,  $n = 3$ ;  $> 1$  to 10 g,  $n = 3$ ;  $> 10$  to 100 g,  $n = 10$ ;  $> 100$  to 1000 g,  $n = 27$ ;  $> 1000$  g,  $n = 18$ ). The mean total length and weight of fetuses were 347 mm ( $\pm 148$ ) and 626 g ( $\pm 551$ ,  $N = 17$ ) for males, and 371 mm ( $\pm 137$ ) and 649 g ( $\pm 515$ ,  $N = 31$ ) for females. The mean weight and total length of the mothers of male and female pups were 19.7 kg ( $\pm 3.1$  kg), 122.0 cm ( $\pm 7.9$  cm,  $N = 17$ ) and 20.0 kg ( $\pm 2.7$  kg), and 125.4 cm ( $\pm 5.6$  cm,  $N = 32$ ), respectively, and did not differ significantly ( $P > 0.1$ ).

## Discussion

### Age at sexual maturity

Female sea otters from south-central Alaska are capable of becoming reproductively mature at age 2 (30%), with the majority mature by age 3 (73%). By analyzing reproductive tracts, Kenyon (1969) and Schneider (1973b) estimated age at sexual maturity to be 3–4 years for sea otters in the Aleutian Islands. Through visual observations of marked known-age sea otters, Miller (1974), Wendell et al. (1984), and Jameson and Johnson (1993) concluded that most sea otters mature at 4 years of age in California, but Jameson and Johnson (1993) also reported that some (two of nine; 22%) females became mature in their third year (age 2). Garshelis et al. (1984) and Jameson and Johnson (1993) also visually estimated sexual maturity at age 4 in a small sample from western Prince William Sound, but maturity may also occur earlier in Alaska, as Monson and DeGange (see footnote 2) visually observed female sea otters pupping at age 2 at Kodiak Island. Compari-

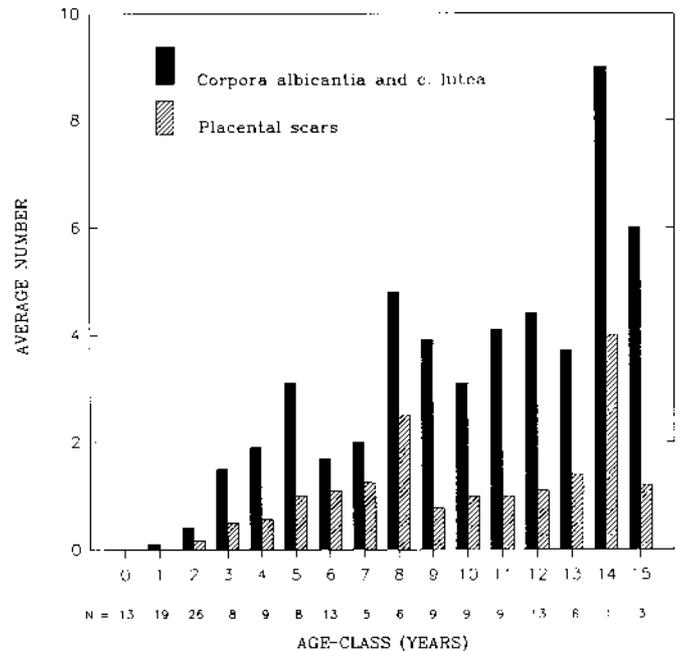


FIG. 1. Placental scars and ovarian structures by age-class of female sea otters.

sons of our results with those cited above suggest that female sea otters can attain sexual maturity in some populations at age 2. Visual detection of maturity at age 2 may require a relatively large sample, particularly if primiparous females are more likely to lose their offspring than multiparous females (Monson and DeGange, see footnote 2).

### Age-specific reproduction

Our maximum estimates of annual reproduction were 0.88 for 8- and 9-year-old females and 0.84 for all sexually mature females, which are similar to estimates from Amchitka Island (88%) (Kenyon 1969, revised by Jameson and Johnson 1993), and California (85–94%) (Siniff and Ralls 1991; Jameson and Johnson 1993), where estimates resulted from observing individuals over time. These comparisons suggest that annual reproductive rates may not vary greatly among those populations studied and that estimates of reproductive rates obtained from visual observations of marked animals in the wild and the analysis of reproductive tracts are comparable. The decline in the reproductive rate of 14- and 15-year-old females may represent the initiation of reproductive senescence in this species or was perhaps simply the result of having a small sample of old animals.

### Size and sex ratio of fetal sea otters

Our measures of fetal size and the recent reproductive history of female sea otters support the descriptions of a broad seasonal reproductive cycle for sea otters in Alaska (Kenyon 1969; Garshelis 1984). Although pups may be born at any time of the year (Kenyon 1969), the reproductive cycle in Alaska is characterized by a peak parturition period beginning in March and extending through July. Weaning of pups and breeding follow about 6 months after parturition. Of the sexually mature females we examined, 16% were lactating, indicating a dependent pup, while 56% were pregnant. Most fetuses (45 of 61) were in the two largest size classes, weighing, on average, 779 g, while six of 61 were in the two smallest classes ( $< 10$  g). If reproductive events are typically

distributed evenly throughout the year, with a 6-month gestation and 6-month dependency period, as described by Jameson and Johnson (1993), we would have expected fetuses to be represented equally in each fetal size class and approximately equal proportions of pregnant and lactating females should have been present. Our data indicate that the oil-spill related mortality that provided the otters for our study occurred shortly before a peak in pupping was to have occurred.

Kenyon (1969) assumed a 1:1 sex ratio among 58 sea-otter fetuses (26:32). K.B. Schneider (personal communication) described a 1:1.3 fetal sex ratio that was significantly biased in favor of females among 261 fetuses (112:149) recovered from otters from the Aleutian Islands. Our results also demonstrate a significant deviation from parity in the sex ratio of fetal sea otters. Among some polygynous mammals, according to a sex allocation theory developed by Trivers and Willard (1973), females should produce more male pups when their body condition is good and stored reserves are high. This provides male offspring with the potential for greater reproductive effort, the gender with the greater reproductive potential in most polygynous mammals (Clutton-Brock et al. 1982; Le Bocuf and Reiter 1988). Conversely, females in poor condition should produce more female pups. Empirical evidence has been gathered that supports this theory for a number of species including bison (*Bison bison*; Rutberg 1986), grey seals (*Halichoerus grypus*; Anderson and Fedak 1987), and deer (Clutton-Brock et al. 1986; Kucera 1991). Other studies have reported results that conflict with Trivers and Willard's theory (Verme 1983, 1985; Skogland 1986). Thomas et al. (1989) provide data that support the theory of sex allocation, but based on the age of the female rather than body condition. He found that young female caribou produced significantly more female fetuses and older females produced significantly more males than expected. We were unable to detect differences in the weights or lengths of mothers of male versus female fetuses or in the sex ratios of fetuses of younger versus older females. However, it is apparent that the overall female bias in the fetal sex ratio results primarily from younger females producing more female than male offspring. The reason for the apparent female bias in the fetal sex ratio in sea otters and how this bias affects sex ratios over time in the adult population is unclear.

#### Sources of error in estimates

Biases in our method of age estimation, particularly in the younger age classes, would potentially have the greatest influence on our results. Ryzanov and Klevezal (1991) concluded that cementum depositions are the preferred structure for estimating age in sea otters but suggested that the first cementum line may be deposited either in the first or second winter of an otter's life, depending on the time of birth relative to winter. The results of our comparison of estimated ages obtained by two independent methods suggest a lack of bias. Results of tooth readings from known-age animals (Schneider 1973a; Pietz et al. 1988) suggest that the method we used to estimate ages is accurate.

A second assumption of this study is that the current reproductive status and sexual maturity of a female sea otter can be determined from examination of carcasses and reproductive tracts. Most (144 of 177) of our samples were classified as pregnant, lactating, or immature, leading to unequivocal classifications. However, at least three conditions offer the possibility of a reproductive status classification error; (1) pregnant-

unimplanted animals may be classified as nonreproductive, (2) a female that has lost a pup during dependency could be considered nonreproductive (if a placental scar was misclassified), or (3) early embryonic mortality may result in a pregnant-unimplanted classification of a nonreproductive female. Because our collection occurred late in the gestation period of most females in the population (Garshelis et al. 1984; Monnett et al. 1991), we found few (15 of 115) mature animals classified as pregnant-unimplanted, and all others were classified as either pregnant, lactating, or nonreproductive, which minimized the potential for the first and third types of error. A recent placental scar is obvious, and the nonreproductive classification was fairly infrequent in our sample, thereby minimizing the second type of potential error in our classification. Careful examination of the uterus for blastocysts could reduce the effect of the third type of error. A fourth potential error in the classification of reproductive maturity could be made if placental scars were missed or became undetectable prior to the next reproductive event. The effect of the first two types of error would be reduced estimates of reproductive rates, while the third type of error would result in overestimation of reproductive rates. The fourth type of error would result in overestimating age at first reproduction. Our analysis of placental scars and ovarian structures suggests that these methods accurately describe only recent reproductive events (within 1 year) and do not reflect a complete reproductive history.

We also assume that sea otter mortality, carcass collection, and carcass management were not biased. To affect our results, a mortality bias would need to differentially affect female otters with reproductive histories and (or) a current reproductive status different from the population. Piatt et al. (1990) suggests that oil spills may not result in biased mortality within the affected population, stating that oil-related mortality does not discriminate between "fit" and "unfit" members of affected populations. Given the amount and spatial scale of spilled oil, the large number of animals killed, and their age-class distribution, we think it is unlikely that a mortality bias that would affect our results existed. We evaluated the assumptions of unbiased carcass collection and management of our sample by comparing the age-class distribution of our sample with the age-class distribution of all carcasses collected following the spill (age-classes included 2 consecutive years and age 0 not included) and found no significant difference ( $P > 0.1$ ,  $\chi^2$ ). This comparison only indicates that our sample of females was not age biased relative to the total sea-otter mortality.

#### Conclusions

The large-scale mortality of sea otters that resulted from the grounding of the T/V *Exxon Valdez* provided a unique opportunity to obtain a detailed view of the reproductive biology of female sea otters. Our results corroborate the results of previous studies of sea otter reproduction based on visual observations of live animals. The sample size in our study provides age-specific reproductive information that is difficult to obtain in observational studies and may be useful in modeling sea-otter population dynamics. The sampling of reproductive tracts requires a large lethal sample of the population that is often impossible to obtain except under unusual circumstances, such as an oil spill. The consequences of future events like the *Exxon Valdez* oil spill may include the mortality of large numbers of animals. Preparation for future events should

include rigorous protocols for the retrieval and management of biological specimens and their subsequent analysis.

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