Exxon Valdez Oil Spill State/Federal
Natural Resource Damage Assessment
Final Report

Age-Specific Reproduction in Female Sea Otters
(*Enhydra lutris*) from Southcentral Alaska:
Analysis of Reproductive Tracts

Marine Mammal Study 6-4
Final Report

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Study History: Marine Mammal Study 6 (MM6), titled *Assessment of the Magnitude, Extent and Duration of Oil Spill Impacts on Sea Otter Populations in Alaska*, was initiated in 1989 as part of the Natural Resource Damage Assessment (NRDA). The study had a broad scope, involving more than 20 scientists over a three year period. Final results are presented in a series of 19 reports that address the various project components. A journal article based on this report has been published (Bodkin, J. L., D. M. Mulcahy, and C. J. Lensink. 1993 Age-specific reproduction in female sea otters (*Enhydra lutris*) from southcentral Alaska: analysis of reproductive tracts. Canadian Journal of Zoology 71(9):1811-1815.).

Abstract: We estimated age of sexual maturity and age-specific reproductive rates by examining carcasses and reproductive tracts from 177 female sea otters (*Enhydra lutris*). Carcasses were recovered from southcentral Alaska, primarily western Prince William Sound, following the T/V *Exxon Valdez* oil spill in 1989. Sexual maturity was first reached at age two. The proportion of sexually mature animals increased from 30% at age two to 100% at age five. Annual reproductive rates increased from 22% at age two to 78% at age five and remained relatively stable (75-88%) through age 15. The sex ratio of 55 fetal sea otters was 18 male:37 female and significantly differed from parity. Females younger than eight 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 in the literature based on *in situ* observations of marked individuals.

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EXECUTIVE SUMMARY

We estimated age of sexual maturity and age-specific reproductive rates by examining carcasses and reproductive tracts from 177 female sea otters (*Enhydra lutris*). Carcasses were recovered from southcentral Alaska, primarily western Prince William Sound, following the T/V *Exxon Valdez* oil spill in 1989. Sexual maturity was first reached at age two. The proportion of sexually mature animals increased from 30% at age two to 100% at age five. Annual reproductive rates increased from 22% at age two to 78% at age five and remained relatively stable (75-88%) through age 15. The sex ratio of 55 fetal sea otters was 18 male:37 female and significantly differed from parity. Females younger than eight 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 in the literature based on *in situ* observations of marked individuals.

INTRODUCTION

Age-specific reproductive rates are important variables in the dynamics of long-lived mammal populations (Caughley 1977, Eberhardt 1985), and may respond to habitat quality and availability of resources (Bronson and Rissman 1986, Bronson 1989, Garrott et al. 1991). Also, 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 observations 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[1]) and by analysis of reproductive tracts of dead animals (Kenyon 1969, Schneider 1973a, Sinha et al. 1966). Previous studies have been conducted at sites in Alaska and California, enabling comparisons of reproductive characteristics among populations. Our objectives in this study were to: 1) estimate age-specific reproduction in sea otters from southcentral Alaska, 2) compare the results of reproductive studies using reproductive tracts and visual observations of live animals, and 3) examine the assumptions associated with methods of estimating reproductive characteristics in female sea otters.

METHODS

We examined 177 reproductive tracts from female sea otters recovered during the response to the T/V *Exxon Valdez* oil spill in Prince William Sound, Alaska. Only reproductive tracts where tissue quality was adequate and the carcass recovery location was known were used. Animals were collected from 30 March to 30 August 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 a premolar tooth (Garshelis 1984, Pietz et al. 1988). At least four sections were prepared and read from each tooth by Matson's Laboratories (Box 308, Milltown, MT). No birth date was assumed in the interpretation of the annuli, only that deposition occurred during winter. To evaluate our age estimates, a sample of 29 two and three year old otters (as estimated by Matson) was aged according to 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 two were estimated at age three by Lensink's method, and four animals that Matson aged at three were aged at two years by Lensink's method. The estimated ages obtained from each of these methods were compared using the Wilcoxon ranked sign 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. Reproductive tracts were preserved in 10% formalin following removal from fresh or frozen

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[1]In prep. Reproduction and survival of sea otters at Kodiak Island, Alaska.

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carcasses. Uteri were opened and the presence of embryos and fetuses were noted and their lengths, weights, and sex recorded. Fetuses were classified into five weight classes (< 1 g, > 1 to 10 g, > 10 to 100 g, > 100 to 1,000 g, and $> 1,000$ g) (Kenyon 1969).

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 lumenal 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 six 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: 1) pregnant-implanted (fetus or embryo present), 2) pregnant-unimplanted (corpus luteum present but no indication of embryo or fetus), 3) lactating (had dependent pup at or near time of death), and 4) 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 morphological similarity of the post-fertilization 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: 1) nulliparous (not pregnant and no placental scars or ovarian structures), 2) primiparous (presence of a single scar or structure, embryo, fetus or lactation), or 3) 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 in each age class.

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 (64%) 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 of mature females (48.5,

49.6, 48.8, and 48.7 cm, ages 2-5, N = 44) was significantly greater (P < 0.001, t-test) than the mean length of immature females (42.4, 45.5, and 45.0 cm, ages 1-4, N = 62).

The proportion of females reproductively mature increased from 0.30 at age two (in their third year of life) to 0.73 at age three. All animals aged five or older except one were considered mature (Table 1). Annual reproductive rates increased from 0.22 at age two to 0.88 for ages eight and nine and varied slightly for animals older than nine (Table 1). In 97 of the 115 (84%) reproductively mature animals, sexual maturity was verified by pregnancy or lactation, and placental scars indicated maturity in the remainder. All lactating females had a placental scar. The reproductive rates for all females ≥ age three, ≥ age four, and ≥ age five years old, and finally, for all sexually mature females were 0.80, 0.82, 0.83, and 0.84 respectively. The reproductive rate of the oldest age class of females (14-15 yrs) declined to 0.75; however, only eight females were represented in this age class.

Placental scars were first observed in two-year-old female sea otters (Figure 1). The mean number (± = standard deviation) of placental scars observed in each pair of uterine horns increased from 0.17 (± 0.39) at age 2, to 0.50 at age 3 (± 0.76), and 0.57 (± 0.53) at age 4, and averaged 1.2 (± 0.96) for all older age classes with the exception of age 9 when the mean was 0.78 (± 0.67). A maximum of five placental scars was observed in one eight year old animal.

Ovarian structures (corpora lutea and corpora albicantia) were observed in two of 19 one-year-old females (Figure 1). The mean number of ovarian structures generally increased from 0.11 (± 0.31) at age one to 3.12 (± 2.59) at age five then fluctuated from 1.7 (± 0.63) at age six to 6.0 (± 2.0) at age 15. A maximum of nine ovarian structures were observed in two females, aged at 8 and 14 years.

Sixty-one fetuses were recovered from 64 pregnant otters. The sex ratio of 55 fetuses that could be sexed was 18 male to 37 female (1:2.1), which significantly differed from parity (P < 0.02; chi square test). There was a trend toward younger females producing female offspring and older females producing male offspring. The sex ratio of 27 fetuses of females age seven or younger was 1:2.9 significantly favoring females (P < 0.02). The sex ratio of 22 fetuses of females age eight and older did not differ from parity. 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 1,000 g, n = 27; > 1,000 g, n = 18). The mean total lengths and weights of fetuses were 350 mm (± 14.4), and 658 g (± 549) for males, and 372 mm (± 13.6), and 659 g (± 506) for females. The mean weights and total lengths of the mothers of male and female pups were 20.1 kg (± 7.8 kg), 48.1 cm (± 3.0 cm), and 20.0 kg (± 6.3 kg), 49.3 cm (± 2.2 cm), respectively, and did not significantly differ (P > 0.1).

DISCUSSION

Age of Sexual Maturity

Female sea otters from southcentral Alaska are capable of becoming reproductively mature at age two (30%), with the majority mature by age three (73%). Kenyon (1969) and Schneider (1973a) estimated age of sexual maturity at three to four years for sea otters in the Aleutian Islands by analyzing reproductive tracts. Miller (1974), Wendell et al. (1984), and

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Jameson and Johnson (1993) using visual observations, concluded that most sea otters mature at four 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 two). Garshelis et al. (1984), and Jameson and Johnson (1993) also visually estimated sexual maturity at age four in a small sample from western Prince William Sound, but maturity may also occur earlier in Alaska, as Monson and Degange[1] visually observed female sea otters pupping at age two at Kodiak Island. Comparisons of our results with those cited above suggests that sexual maturity can be reached by age two. Visual detection of maturity at age two may require a relatively large sample, particularly if primiparous females are more likely to lose their offspring than multiparous females (Monson and DeGange[1]).

Age-specific Reproduction

Our maximum estimates of age-specific rates were 0.88 for eight and nine year olds and 0.84 for all sexually mature females. Our estimates of annual reproduction for mature female sea otters, based on the analysis of reproductive tracts, are similar to estimates from Amchitka Island (0.88) (Kenyon 1969, revised by Jameson and Johnson 1993), and California (0.85-0.94) (Siniff and Ralls 1991, Jameson and Johnson 1993), where estimates resulted from observing individuals over time. These comparisons suggest annual reproductive rates may not vary greatly among populations 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 perhaps was simply the result of 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). Whereas pups may be born during any time of the year (Kenyon 1969), the reproductive cycle in Alaska is characterized by a peak birthing 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 an average of 779 g, while six of 61 were in the two smallest classes (< 10 g). If reproductive events were 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 ♀). Schneider (pers. comm.) described a 1:1.3 fetal sex ratio that was significantly biased in favor of females among 261 fetuses (112 ♂:149 ♀) recovered from the Aleutian Islands. Our results also demonstrate a significant variation from parity among the sex ratio of fetal sea otters. Among some polygynous mammals, according to a sex allocation theory

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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 the potential for greater reproductive effort to the males, the gender with the greater reproductive potential in most polygynous mammals (Clutton-Brock et al. 1982, Le Boeuf and Reiter 1988). Conversely, females should produce more female pups when body conditions are poor. 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 supports 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. Although we were unable to detect differences in the weights or lengths of mothers of male versus female fetuses, we did find that younger females conceived more females than males, while the sex ratio of older females did not differ from parity. Because fetuses will influence adult female weights, we first compared mean fetus weights of females less than eight to females greater than seven years old and found no significant differences. We then found that the mean weight of mature females < eight years of age was not significantly different than the mean weight of mature females > seven years of age. 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 suggested a lack of bias. Results of tooth readings from known age animals (Schneider 1973b, Pietz et al. 1988) suggest the method we used to estimate ages is accurate.

A second assumption of this study is that the current reproductive status and sexual maturity can be determined from carcasses and reproductive tracts. Most (144 of 177) of our samples were classified as pregnant, lactating, or immature, leading to unequivocal classifications. Two classifications offer the possibility of a reproductive status error: 1) pregnant-unimplanted animals may be classified as non-reproductive, and 2) a female that has lost a pup during dependency could be considered non-reproductive, if a placental scar was misclassified. Due to the timing of our collection, 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) animals classified as pregnant-unimplanted. All others were classified as either pregnant, lactating, or immature, minimizing the potential for the first type of error. A recent placental scar is obvious, and the non-reproductive classification fairly infrequent in our sample, thereby minimizing the second type of potential error in our classification. A third potential error, in the classification of reproductive maturity, could be made if placental scars are missed or become undetectable prior to the next reproductive event. The effect the

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first two types of error would be reduced estimates of reproductive rates. The effect of the third type of error would result in overestimating age at first reproduction. Our analysis of placental scars and uterine structures suggests that these methods accurately describe only recent reproductive events (within one year) and do not reflect a complete reproductive history.

We also assume that sea otter mortality, carcass collection and carcass management were not biased. For a mortality bias to affect our results it would need to differentially affect female otters with reproductive histories and/or a current reproductive status different from the population. Piatt (1990) suggests 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 numbers of animals killed, and their age class distribution, we feel 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 to the age class distribution of all carcasses collected following the spill (age classes included two consecutive years and age 0 not included) and found no significant difference ($P > 0.1$, chi-square). 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 difficult to obtain in observational studies and that may be useful in modeling sea otter population dynamics. The use 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 such as the *Exxon Valdez* oil spill may include the mortality of large numbers of animals. Preparation for future events should include rigorous protocols for retrieval and management of biological specimens and their subsequent analysis.

ACKNOWLEDGMENTS

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

Age class (yrs)	Reproductive tract analysis				
	Number of females	Proportion pregnant	Proportion lactating	Proportion reproductively mature[a]	Reproductive rate[b]
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

[a] As determined by the presence of placental scars, fetuses, unimplanted embryos or lactation.

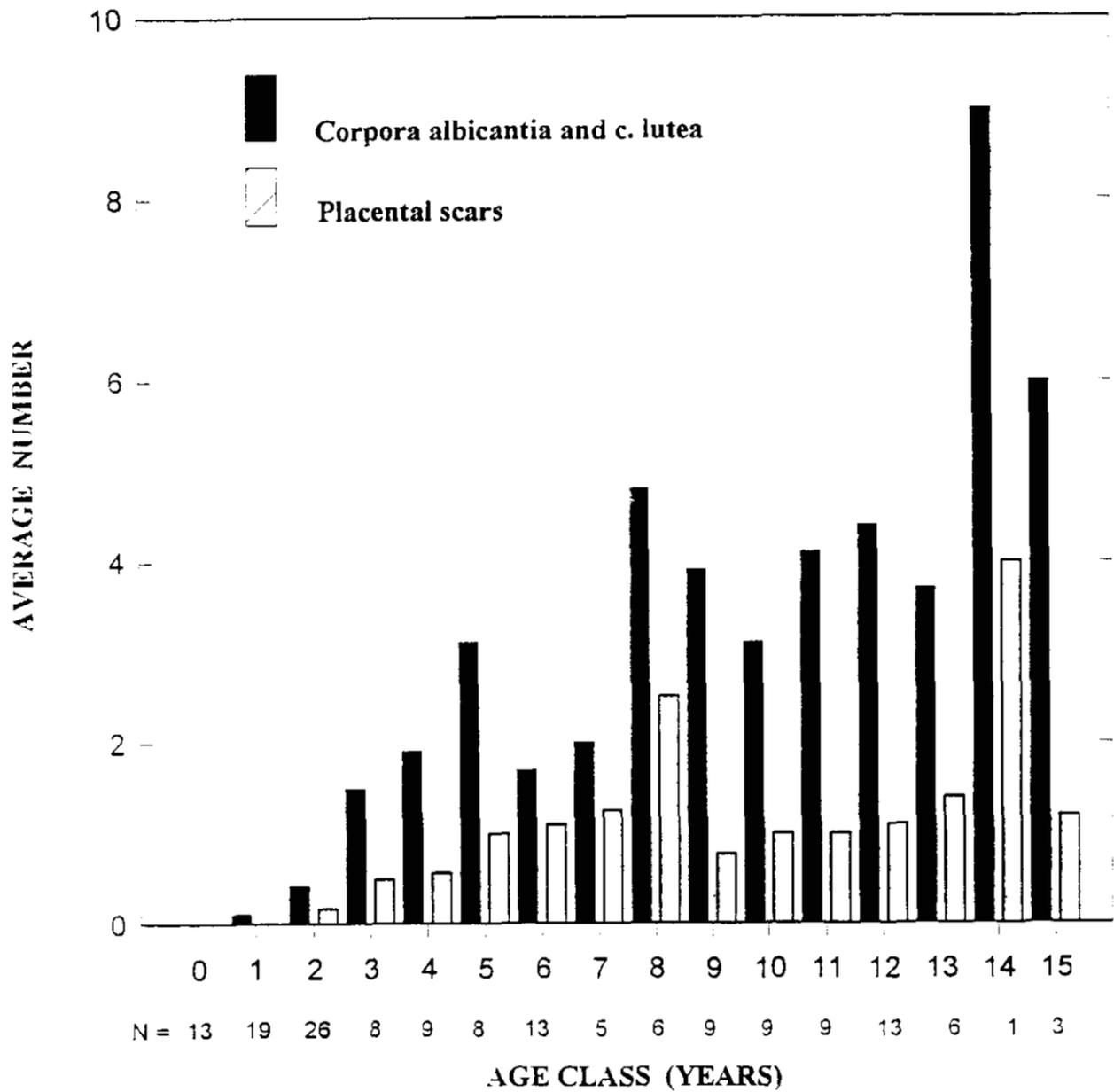[b] As determined by the presence of a fetus, embryo, or lactation.

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