Breeding Patterns and Reproductive Success of California Sea Otters

Marianne L. Riedman; James A. Estes; Michelle M. Staedler; Alisa A. Giles; David R. Carlson

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BREEDING PATTERNS AND REPRODUCTIVE SUCCESS OF CALIFORNIA SEA OTTERS

MARIANNE L. RIEDMAN, Life Sciences Division, Monterey Bay Aquarium, 886 Cannery Row, Monterey, CA 93940
JAMES A. ESTES, National Biological Survey, Institute of Marine Sciences, University of California, Santa Cruz, CA 95064
MICHELLE M. STAEDLER, Life Sciences Division, Monterey Bay Aquarium, 886 Cannery Row, Monterey, CA 93940
ALISA A. GILES, Life Sciences Division, Monterey Bay Aquarium, 886 Cannery Row, Monterey, CA 93940
DAVID R. CARLSON, National Biological Survey, Institute of Marine Sciences, University of California, Santa Cruz, CA 95064

Abstract: Following commercial exploitation in the eighteenth and nineteenth centuries, sea otter (*Enhydra lutris*) populations in Alaska, British Columbia, and Washington recovered at 17–20% a year, yet the California population increased at only 5% a year. This slow rate of increase is perplexing, given that unoccupied and apparently favorable habitats occur throughout the sea otter's California range, and higher growth rates occurred among northern sea otter populations. Better knowledge of the demography of the California population is important in understanding these disparate population growth rates. We studied the reproductive biology and behavior of 53 tagged female sea otters from 1985 to 1991 in Monterey Bay, California. During the study, 136 pups were born to these females. Observations of each female enabled us to determine exact or estimated pup birth dates, which we used to calculate lengths of gestation, pup dependency, and reproductive cycle. Seasonal trends in pupping, in the proportion of adult females with pups, and in pup separations from their mothers were relatively uniform throughout the year. The average interval between separation from pup and subsequent birth was 198 days, the interbirth interval was 407 days, and estimated birth rate was 0.90/year for all adult females. For females that pupped annually (did not lose undetected newborns), the average interbirth interval was 342 days, given an estimated birth rate of 1.07/year. Length of the reproductive cycle increased with increasing length of prior pup dependency. However, the interval between separation from pup and subsequent birth was delayed among females that prematurely lost their pups. The average length of dependency for pups that survived to weaning was 166 days, but ranged from 120 to 280 days. The maximum preweaning survival rate was 0.60–0.65, less than values measured or inferred for some Alaskan populations. Most pups that did not survive to weaning were lost within a month of birth. The probability of successfully weaning pups and the length of dependency increased ($P = 0.077$) with mothers' ages, thus indicating that reproductive success may increase among females with greater mothering experience. The high preweaning pup mortality we observed probably accounts for much of the relatively slow growth rate of the California sea otter population.

The California sea otter (*E. l. nereis*) was classified as "threatened" under the U.S. Endangered Species Act, "depleted" under the U.S. Marine Mammal Protection Act, and a "fully protected mammal" by the state of California. Despite this protection, the population has only increased about 5% a year since 1914, which is slow because unoccupied and apparently favorable habitats exist at both ends of the range, and higher growth rates (17–20% a yr) occur among sea otter populations in Alaska, British Columbia, and Washington (Estes 1990).

The explanation for these disparate population growth rates is rooted in comparative demography (i.e., age and sex composition, age-specific natality, and survival rates). Besides these population parameters, it is important to know

whether reproductive success varies among individuals, which life history parameters contribute to such variation (e.g., offspring survival, natality rate, reproductive life span, mating success), and how reproductive success is influenced by age and environmental factors (Clutton-Brock 1988).

Our study was based on long-term records of reproductive patterns collected from 53 tagged females. The utility of this approach in studies of reproductive success has been demonstrated in recent work on mammals, birds, amphibians, and insects (Clutton-Brock 1988). We were able to assemble reproductive histories from individual females because sea otters are philopatric and often occur close to shore, individuals can be closely observed (especially along the north-

ern Monterey Peninsula), and many otters in Monterey Bay have been tagged and are therefore individually recognizable.

Studies of marked sea otters in California have demonstrated that adult females typically give birth to a single pup each year, average gestation is 4–6 months, and the average length of postnatal dependency is about 6 months (Loughlin et al. 1981, Wendell et al. 1984, Siniff and Ralls 1991, Jameson and Johnson 1993). Although these studies have clarified several life history characteristics of sea otters, they have focused on population averages rather than individual differences. Our study emphasized variation within and among individual sea otters in length of gestation, length of pup dependency, interbirth interval, natality, preweaning survival, and the effect of age on female reproductive success. We provide data confirming high preweaning loss rates of sea otters in California compared with those in Alaska (Siniff and Ralls 1991), and note the implications of these findings to the dynamics of the California sea otter population.

STUDY AREA AND METHODS

Divers using either scuba or rebreathers and a Wilson trap (Ames et al. 1986) captured sea otters. Colored plastic tags inscribed with numbers (Temple Orig. cattle ear tag, Temple, Tex.) were attached to the interdigital webbing of both hind flippers, enabling observers to identify otters from shore, on the basis of tag color and interdigital position (Ames et al. 1983).

We made most observations of tagged females between Point Pinos (36°38.5′N, 121°56′W) and Del Monte Beach (36°36′N, 121°53′W) on the northern Monterey Peninsula, with 10 × 40 binoculars and 50–80× spotting scopes. We also occasionally observed otters at other locations between Santa Cruz and Point Lobos State Reserve. We located most tagged otters at least once a week, although we sighted the majority of individuals more frequently. When a female was located, we recorded presence or absence of a pup and evidence of estrus or recent mating (e.g., pairbonding, copulation, or a recently injured nose; Foott 1971).

We observed 53 adult females that produced 136 pups between 1985 and 1991. The period of time each otter was observed varied because some individuals died, lost their tags, or were tagged later in the study. Prior to 1985, a few individuals were tagged and observed sporadically by the California Department of Fish and Game, and we continued to monitor these animals. The analysis of seasonality of pupping included 7 additional pups born to these females in the early 1980s.

Females of known or estimated age were those that had been tagged as dependent pups, or occasionally as recently weaned juveniles (weighing ≤13.6 kg), whose birth dates were estimated to be 1 year prior to capture. We estimated minimum ages of females tagged as adults between 1976 and 1991 to be ≥3 years plus the time interval since the animal was tagged.

Using each pup's known or estimated birth and separation dates, we calculated the length of 3 reproductive events: gestation, pup dependency, and reproductive cycle. Length of gestation was the interval between the last date we observed a female with her pup before separation and the first date she was sighted with a new pup. Length of pup dependency was the interval between a pup's birth date and the last date it was observed with its mother before weaning. Length of the reproductive cycle was the interval between successive births for each female. We tested variation among individual females in mean length of dependency and mean length of gestation, using 1-way analysis of variance (ANOVA).

We used methods similar to those employed by Siniff and Ralls (1991) to measure and analyze seasonality of births and mother-pup sep-
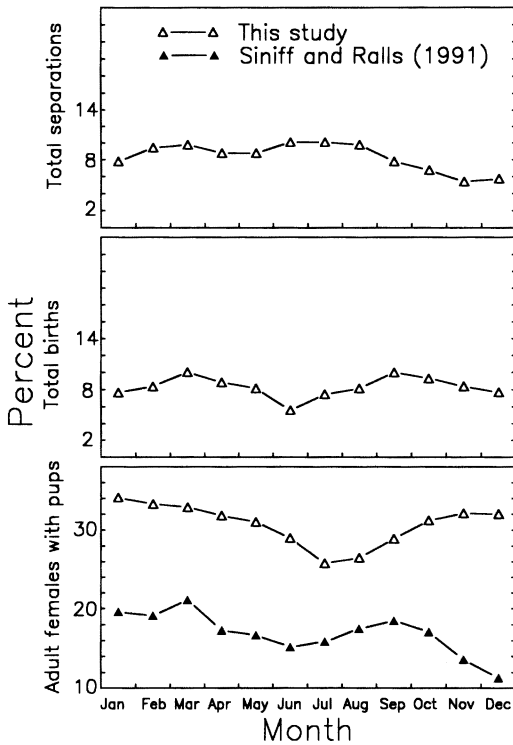
Fig. 1. Seasonality of the percent of adult female sea otters accompanied by pups, observed births, and mother-pup separations in Monterey Bay, California, 1985–91, including data from Siniff and Ralls (1991) from the Big Sur coast of central California.

Fig. 2. Distribution of the length of sea otter pup dependency periods ($n = 147$ pups) in Monterey Bay, California, 1985–91. The assumed minimum age of survival was 120 days. The shaded area on the first bar represents additional pups probably lost at birth that we did not observe ($n = 11$).

arations. We scored adult females as being accompanied by a pup during a given month if they were known to have been with a pup on more than half the days. We then calculated the proportion of females that were observed with pups for each month. In 99 of 143 births, sightings were made of the mother during ≥ 2 consecutive months at the time of separation (weaning or pup loss). In these cases, we estimated date of separation as the midpoint between when she was last seen with the pup and first seen without it.

RESULTS

Seasonality of Births and Mother-Pup Separations

The number of births that occurred in any given month ranged from 5 to 10% of the total of 143 pups born (Fig. 1). Although the number of births was largest in March and September and smallest in June, the seasonal pattern was not different from uniform (Kolmogorov-Smir-
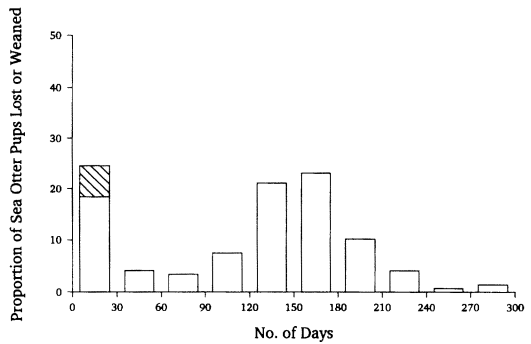
nov test, $D_{max} = 0.052$, $P > 0.20$, $n = 143$). The proportion of females accompanied by pups each month was weakly seasonal, ranging between 34.1% (SE = 2.3, $n = 411$) in January and 25.8% (SE = 2.1, $n = 422$) in July. This pattern differed from that reported by Siniff and Ralls (1991) for sea otters near the center of their California range in that the average proportion of adult females accompanied by pups was nearly 14% greater in Monterey Bay and our data indicated no autumn decline in the proportion of mothers with pups (Fig. 1).

The number of separations that occurred during any given month ranged from 5 to 10% of the total (Fig. 1). The seasonal pattern of separations, although modest, was different from uniform (Kolmogorov-Smirnov test, $D_{max} = 0.089$, $P < 0.01$, $n = 99$), and slightly higher from February through August.

Pup Dependency

The average length of association between pups and their mothers was 120 days (range 1–280 days). Forty-six of these pups (34%) were separated from their mothers (weaned or lost) at <120 days (Fig. 2). We assumed that all or most of these pups died. Of 90 pups that remained with their mothers ≥ 120 days, the average length of dependency was 166 days (5.5 mon.). We assumed that these pups were weaned successfully. Seven tagged pups weaned between 120 and 150 days of age are known to have survived, 5 to adulthood.

Length of dependency ranged from 120 to 280 days among the 90 pups that we assumed survived to weaning. Mean lengths of depen-
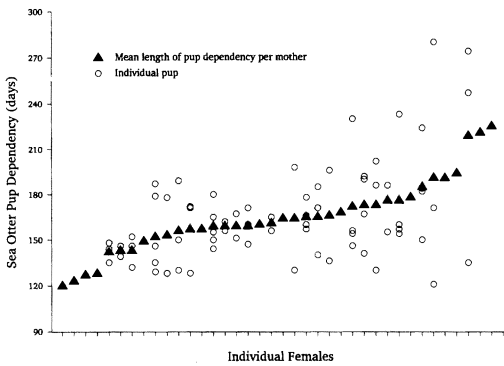
Fig. 3. Estimated mean lengths of dependency for 90 pups born to 38 female sea otters in Monterey Bay, California, 1985–91.

Fig. 5. Length of sea otter pup dependency period versus the time between maternal separation from pup to the following birth (*n* = 65 pups) for sea otters in Monterey Bay, California, 1985–91. Open circles represent cases for which we suspect an interceding birth was missed by the observer or skipped by the mother. Lines are least-squares best linear fits. The solid line = all data (*r*² = 0.052, *P* = 0.068), the top dashed line = open circles (*r*² = 0.955, *P* < 0.001), and the bottom dashed line = closed circles (*r*² = 0.299, *P* < 0.001).

dency among the 38 females that produced these pups (1–6 pups/F) varied from 120 to 225 days (Fig. 3). Among 33 of these females that produced ≥2 pups, mean length of pup dependency for each female differed (*F* = 1.64; 31, 83 df; *P* = 0.04).

Gestation

The mean interval between weaning and copulation was 1.3 days (range 0–20, *n* = 40). Estrous females copulated with 1–3 different males during a single estrous period. Because we considered date of separation between mother and pup to represent onset of estrus as well as time of conception, estimates of gestation length may be biased high by several days for some females.

Mean length of gestation was 198 days (*n* = 61 pups from 23 F), although as with length of pup dependency, variation occurred within and among individual females (Fig. 4). Length of
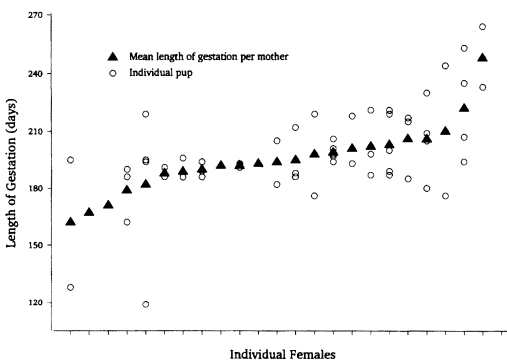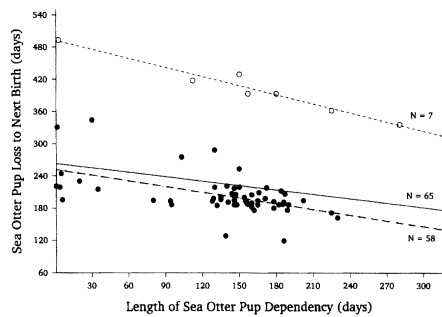
gestation ranged from 119 to 264 days for individual pups, while means among females ranged from 162 to 249 days. Nonetheless, length of gestation among females for which we had ≥2 estimates did not differ (*F* = 1.40; 21, 38 df; *P* = 0.18).

Interbirth Interval and Birth Rate

The average interbirth interval (length of reproductive cycle) for 86 pups born to 32 females was 407 days: an annual birth rate for adult females of 0.90/year. The mean interbirth interval for all females, including those that did not pup annually because they either lost unobserved pups or skipped births in certain years, ranged from 238 to 1,119 days. Of 69 pups born to females (*n* = 28) that pupped on an approximate annual basis (were known to have not lost undetected newborns), the mean interbirth interval was 342 days, giving a birth rate of 1.07/year.

As expected from the relationship between length of reproductive cycle and length of pup dependency, the interval from pup loss to the subsequent birth (Fig. 5) declined with length of pup dependency. However, data appear to cluster in 2 groups (Fig. 5). We speculate that we missed some births (the most likely possibility) or birth events were skipped by the mother, because the best linear fit to these data was displaced upward by about 200 days, which is close to the mean length of gestation (198 days) (Fig. 5). If we assumed that all of these cases (open circles in Fig. 5) represent births missed by observers, then about 11% (7 of 65)

Fig. 4. Estimated lengths of gestation for 61 pups born to 23 individual female sea otters in Monterey Bay, California, 1985–91.

of the term pregnancies were undetected, thus providing a natality rate for adult females of about 1.01/year. This estimate is close to the birth rate of 1.07/year estimated from the average interbirth interval of 342 days for females that pupped about once each year and did not lose undetected newborns.

Length of the reproductive cycle increased with an increasing length of prior pup dependency (Fig. 6). In addition, females that pupped annually and did not successfully wean their pups (i.e., the dependency period was ≤120 days) had shorter ($t = 3.97$, 19 df, $P < 0.001$) mean reproductive cycles (298 days, $n = 15$) than did successful females (359 days, $n = 23$), indicating that most females that lost pups entered estrus and became pregnant again earlier than if they had successfully weaned their pups. For example, 1 female gave birth to 5 pups during the study; she lost 2 pups 1 day after birth, and in both cases her subsequent reproductive cycle was 222 days. In contrast, the lengths of her reproductive cycles following 3 successfully weaned pups were 344, 350, and 354 days.

If length of the reproductive cycle is equivalent to mean length of gestation plus length of pup dependency, then length of pup dependency plotted against length of the subsequent reproductive cycle should follow a line that originates at y = 198 days (i.e., when length of dependency equals zero) and increases linearly with slope = 1 (Fig. 6). However, the linear best fit line to our data (Fig. 6) had a greater y-intercept ($t = 7.14$, 68 df, $P < 0.001$) and lower slope ($t = 6.56$, 67 df, $P < 0.001$) than the expected function. Thus, measurements of reproductive cycle length tended to be greater (and more variable) than expected when pups were lost early. This departure was most pronounced (reproductive cycle about 75 days longer than expected) for females whose pups were lost in their first month.

The longer and more variable reproductive cycles for females that prematurely lost pups may be due to a delay in onset of estrus or repeated estrous cycles, delaying onset of successful gestation. The mean interval between mother-pup separation and the first observed evidence of mating was 11.8 days (SD = 9.9, $n = 15$) for females that prematurely lost pups (at <120 days of age), and 1.3 days (SD = 4.0, $n = 40$) for females that successfully weaned pups. Most females (83%) that successfully weaned
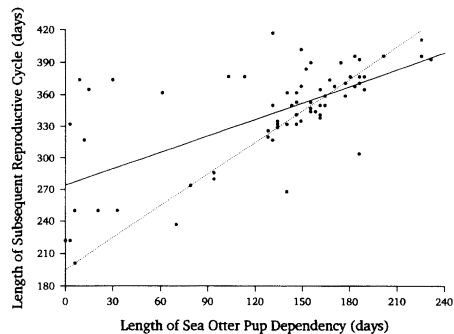

Fig. 6. Length of pup dependency period versus length of subsequent maternal reproductive cycle of sea otters in Monterey Bay, California, 1985–91 ($n = 69$ pups). Dotted line (y = 198 + x) is the expected relationship if females are always impregnated at the time of pup loss. Solid line is the linear best fit to the data (y = 270 + 0.52x; $r^2 = 0.43$, $P < 0.001$, $n = 69$).

pups were observed mating or pairbonded the same day they were first seen without a pup, while only 2 of 15 females that lost pups were seen mating the same day they were first observed without a pup; these 2 cases involved females that lost older pups (94 and 113 days of age). In addition, a few females apparently entered repeated estrous cycles over the course of a few weeks to a few months before becoming pregnant again.

Pup Survival

Thirty-five percent of the 136 pups born remained with their mothers <120 days and were assumed to have died. There were 11 additional cases in which frequently observed tagged females apparently lost their pups at or near the time of birth. These females entered estrus and mated at about the time they were scheduled to give birth; their pupping schedule was based on prior observations indicating the dates when these females weaned their previous pup and mated. The addition of these animals increases the preweaning mortality estimate to 40% (SE = 4.0, $n = 147$). Preweaning mortality was probably even higher because ≥7 additional females either skipped years between pupping or lost their pups but were not observed closely enough to determine if there was subsequent estrus and mating. Furthermore, some pups that remained with their mothers ≥120 days may have died before weaning. Thirty-six (62%) of the 58 pups that were thought to have died prior to weaning were lost before 30 days of age (Fig. 2). This represents 25% of observed births.

Reproductive Success Versus Female Age

The proportion of pups successfully weaned increased with their mothers' ages. Preweaning pup survival rates were 0.40 for 3- to 6-year-old females ($n = 5$), 0.75 for 7–10 year olds ($n = 12$), and 1.00 for 11–14 year olds ($n = 4$). Length of pup dependency also increased with increasing age of the mother. The mean length of pup dependency was 82 days for 3–6-year-old mothers, 119 days for 7–10 year olds, and 174 days for 11–14 year olds. The linear regression of length of dependency versus mother's age had a positive slope ($t = 1.87$, 19 df, $P = 0.077$, $r^2 = 0.155$).

DISCUSSION

Seasonality of Pupping

The absence of a distinct seasonal birth pattern for sea otters in our study contrasts with the conclusion that there is a primary birth peak in late winter and a secondary peak in late summer through early fall in California (Fisher 1940, Vandevere 1970, Sandegren et al. 1973, Estes and Jameson 1983, Jameson 1989, Siniff and Ralls 1991). Prior analyses, however, were calculated from the proportion of mothers accompanied by pups recorded during surveys or sightings of marked animals, whereas our findings were calculated from pups' birth dates. Our data also indicated a higher proportion of adult females with pups than reported for the southern and central part of the sea otter's range in California (Siniff and Ralls 1991). This difference could result from either a higher birth rate or better preweaning survival in Monterey Bay. In addition, Siniff and Ralls' (1991) data indicated a decline in the proportion of adult females accompanied by pups from October through December, whereas we found a slight increase during this period. Pup survival on the exposed outer coast of central California may be more seasonal (corresponding with winter storms) and lower than in the calmer waters of Monterey Bay. Adult males also remain on their territories throughout the year in Monterey Bay (Loughlin 1980; Riedman and Estes 1990; Riedman, unpubl. data), but only during summer through fall in the southern part of the range (Jameson 1989). This difference in male behavior may result from regional differences in the seasonal probability of males encountering estrous females.

Pup Dependency, Gestation, and Interbirth Interval

The mean dependency period of 166 days (5.5 mon.) recorded for pups in this study is similar to the 6-month estimate reported for California females (Estes and Jameson 1983, Payne and Jameson 1984, Jameson and Johnson 1993) and the 5.5-month dependency for females in Prince William Sound, Alaska (C. W. Monnett, *Enhydra* Res., Homer, Alas., pers. commun.). Although it has been assumed that pups weaned at <150 days (5 mon.) were lost (Payne and Jameson 1984, Siniff and Ralls 1991, Jameson and Johnson 1993), several pups weaned as early as 120 days during our study survived. We also found a wider range of individual variation in the duration of successful pup dependency (120–280 days, or 4.0–9.2 mon.) than had been reported in California (5.0–8.5 mon.; Loughlin et al. 1981, Wendell et al. 1984, Jameson and Johnson 1993). Monnett and Rotterman (1988, unpubl. data) found that the duration of successful dependency periods ranged more broadly still in Prince William Sound (2–11 mon.). Although the cause of this variation is unknown, Monnett and Rotterman (1988) speculated that it was due to differences in food abundance or female condition.

The mean interbirth interval of 407 days (13.4 mon.) we found confirmed the pattern of approximate annual pupping believed to be characteristic of California sea otters, reported as 11–14 (Wendell et al. 1984), 12.8 (Siniff and Ralls 1991), and 12–13 months (Jameson and Johnson 1993). Our estimate corresponds with a birth rate for adult females of about 0.90/year, nearly identical to that reported by Jameson and Johnson (1993) for California females in the southern part of the range.

The average reproductive cycle for mothers that lost their pups was shorter than that of mothers that successfully weaned their pups. This conflicts with Siniff and Ralls' (1991) report of no correlation between length of dependency and the subsequent interbirth interval, although they were surprised by this and noted that further studies on factors affecting length of the reproductive cycle were needed. We also found that reproductive cycles were longer and more variable than expected for females that lost their pups in the month following birth, which could be the consequence of (1) a delay in the onset of estrus, (2) normal onset of estrus without con-

ception, causing the female to go through ≥1 additional estrous cycle before being impregnated, (3) an extended period of unimplanted pregnancy, or (4) an extended period of implanted pregnancy.

Our findings suggest that the longer and more variable reproductive cycles of females that lost pups were due to the first two possibilities. Females that lost pups before minimum weaning age (≥120 days), on average, came into estrus and mated about 11 days later than females that successfully weaned their pups. In addition, some of these females came into estrus and mated ≥2 times during periods of several weeks to several months (thus apparently undergoing recurrent estrous cycles until they were successfully impregnated). These findings are consistent with those of Brosseau et al. (1975), who reported that captive sea otters from Alaska remained in estrus for about 5 days, but if conception did not occur they came into estrus again within 5 weeks.

Effect of Female Age on Pup Survival and Dependency

Female reproductive success tends to increase with age in numerous birds and mammals (Altmann et al. 1988). This pattern, although apparent from our data on the length of association between pups and females of known age, was only marginally statistically significant because of small sample size and high variation among individuals. Mammalian reproductive success is often lowest among the youngest and oldest females (Sherman 1976, Hrdy 1977). However, the probability of successfully weaning pups in sea otters apparently continues to increase with age. A similar pattern of increased reproductive success with age was found in northern elephant seals (*Mirounga angustirostris*) (Reiter et al. 1981). Because parental experience is important in successfully raising offspring in numerous mammals and birds (Riedman 1981), experience in mothering also may be an important component of reproductive success in sea otters.

Pup Survival and Rate of Population Change

The maximum rate of population increase (r_{max}) for sea otters has been estimated at 20% a year on the basis of Cole's (1954:117) algorithm and available estimates for its specified life history parameters (Estes 1990). This is comparable with observed rates of population increase in Washington, British Columbia, southeastern Alaska, and the Aleutian Islands, but is 3–4 times greater than the 5–6% a year rate of population increase in California. The disparity in growth rates between Alaska and California populations apparently is the result of differences in mortality rather than natality. Natality rates of ≥0.90 pups/year have been reported for adult female sea otters in California (Siniff and Ralls 1991, Jameson and Johnson 1993, this study) and Prince William Sound, Alaska (Monnett and Rotterman 1988). Although there are no data on mortality from the rapidly increasing northerly populations described by Estes (1990), the death rate from birth to senescence in these populations may be low given that observations of population increase are close to r_{max} and current estimates of female natality and age at sexual maturity (Riedman and Estes 1990) are correct. Thus, the high rate of preweaning mortality in California sea otters probably is an important contributing factor to the slow rate of population increase.

A caveat to this conclusion is that published female natality rates of 0.90/year probably are biased low, and at least in California may be as high as 1.07/year. The lower figure assumes an equivalence between successful impregnation and visual confirmation of the subsequent birth, whereas the higher figure is derived from the assumption that about 15% of impregnated females go undetected, either because of failed pregnancies or early postnatal mortalities. The fact that we could not maintain constant vigilance on all study animals allows for the possibility that some early postnatal mortalities were undetected. In addition, some females for whom we suspect failed pregnancy or early postnatal mortality were seen copulating at the expected time of birth or observed with a swollen, bloody nose (a definitive sign that she had entered estrus and copulated). The consequence of this possible bias is that published values of r_{max}, all of which are based on natality rates of 0.90/year, also may be biased low. If so, this also helps resolve a paradox: i.e., sustained rates of increase at r_{max} documented and published for several sea otter populations allow for virtually no natural mortality from birth to senescence, even though such mortality occurs.

The variable age of successful weaning (120–280 days) together with the bimodal distribution

of mother-pup separations versus time following birth precludes us from making a precise estimate of preweaning mortality. Siniff and Ralls (1991) found a similar bimodal distribution for the amount of time that pups remained with their mothers, with most females losing pups <80 days after giving birth. They assumed that pups remaining with their mothers <150 days were not weaned successfully, from which they estimated a preweaning mortality rate of 0.42–0.54. However, we found that several pups weaned between 120–150 days survived. Jameson and Johnson (1993) reported that 36% of the pups they observed had separated from their mothers before 150 days of age, although their less frequent observations and assumption that pups <150 days did not survive make it difficult to compare their findings with ours. Although some animals remaining with their mothers <120 days may have been weaned successfully, we have no records of such cases. The overall proportion of mother-pup separations was relatively low from 60 to 120 days of age, so these cases would not greatly affect the preweaning mortality estimate. Conversely, some pups that remained with their mothers ≥120 days probably were not weaned successfully, and some of the females scored as not giving birth in particular years (from observational records) probably lost their pups shortly after birth. These factors would further increase the preweaning mortality rate (>0.4).

The survival rate of dependent pups appears to be higher in Alaska than in California, although more data from various Alaskan populations are needed. Average preweaning survival rates for Alaskan pups range from 0.85 at Kodiak Island (J. L. Bodkin, U.S. Fish and Wildl. Serv., Alas., pers. commun.) to 0.75–0.87 in Prince William Sound, where pups ≥60–90 days were considered successfully weaned (C. W. Monnett, pers. commun.). Furthermore, pups in Alaska appear capable of surviving on their own at a younger age than do pups in California (min. age = 60–90 days in Alas. vs. 120 days in Calif.), and Alaskan pups also gain mass more rapidly than do pups in California. Although birth mass (about 2 kg) and the average weaning age (5.5 mon.) are similar in these populations, pups in Prince William Sound weigh about 16–20 kg at weaning (C. W. Monnett, pers. commun.) while California pups typically weigh 11–14 kg at weaning. Reasons for the comparatively low rates of preweaning mass gain and survival

in California sea otters are unknown. Determining causes of these differences is critical to understanding the depressed growth rate of the California sea otter population.

MANAGEMENT IMPLICATIONS

Management strategies to help the threatened California sea otter population recover should investigate causes of the elevated dependent pup mortality rate reported here. Contributing factors might include differences between California and Alaska in weather and sea conditions, inbreeding depression (Ralls et al. 1983), environmental contaminants, or energetic constraints (Siniff and Ralls 1991). Environmental pollutants and inbreeding depression may be less important because preweaning survival rates tend to increase among older females with greater mothering experience. However, female cetaceans and pinnipeds can impart large amounts of PCBs to their offspring during lactation (Tanabe 1988), and Cockcroft et al. (1989) presented evidence suggesting that in bottlenose dolphins (*Tursiops truncatus*) the majority of the mother's PCB load is transferred to her first-born calf through lactation. We do not know if a similar pattern of transferring the highest pollutant loads to first-born young exists in sea otters, or if such a transfer might have adverse effects on the survival of young. Nonetheless, this does not preclude the potential importance of maternal experience in successfully raising sea otter pups. If the influence of anthropogenic factors on pup survival is not related to the mother's age, we are left with the possibility that central California may offer a suboptimal habitat to sea otters as compared with northern areas nearer the center of the species' natural range.

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