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REPRODUCTIVE STRATEGIES IN SEA OTTERS  
AT AMCHITKA ISLAND, ALASKA

A thesis submitted in partial satisfaction  
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MASTER OF SCIENCE

in

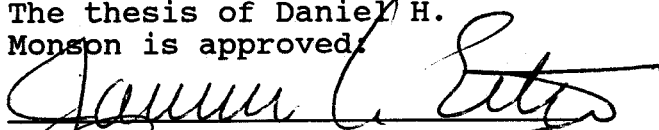
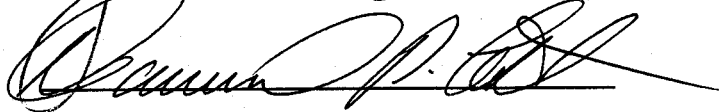

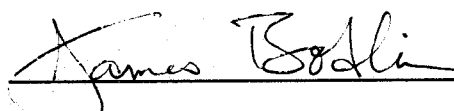
MARINE SCIENCES

by

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## INTRODUCTION

Numerous mammalian species exhibit phenotypic plasticity in reproductive success under varying ecological conditions (Bronson 1989). The driving force behind these variations is the response of individuals to the past and present conditions affecting their current physiological state, as well as the predictability of long-term environmental fluctuations (Negus and Berger 1987, Bronson 1989). When food resources become limiting, age of first reproduction may increase (e.g. columbian ground squirrel, *Spermophilus columbianus*: Dobson and Kjelgaard 1985; red deer, *Cervus elaphus elaphus*: Clutton-Brock et al. 1985; reindeer, *Rangifer tarandus*: Skogland 1985), and birth rates and/or reproductive success may decrease (e.g. Columbian ground squirrel: Dobson and Kjelgaard 1985; red squirrel, *Sciurus vulgaris*: Wauters and Dhondt 1989; arctic fox, *Alopex lagopus*: Angerbjorn et al 1991; red fox, *Vulpes vulpes*: Lindstrom 1989; coyote, *Canis latrans*: Todd and Keith 1983; black bear, *Ursus americanus*: Elowe and Dodge 1989; red deer: Clutton-Brock et al. 1982). Alternatively, the availability of surplus food resources may increase birth rates and success, and lower age of first reproduction (see review by Boutin 1990). Birth rates and success may also be influenced by female age, experience or social status (e.g. elephant seal, *Mirounga angustirostris*: Le Boeuf and Reiter 1988; Sydeman et al. 1991; Cape mountain zebra, *Equus zebra zebra*: Lloyd and Rasa 1989; feral horse, *Equus caballus*: Garrott et al. 1991; see also Riedman 1981, Altmann et al. 1988).

The degree to which a species exhibits phenotypic plasticity in life-history traits is subject to selective pressures working to maximize reproductive potential (Goodman 1979). A central tenet of life-history theory (Fisher 1930), is that reproductive investment incurs a cost which must be balanced against the energetic requirements of growth and maintenance. Costs are expressed in terms of reduced survival and/or future fecundity (Williams, 1966, Pianka and Parker

1975, Clutton-Brock et al. 1983). The balance results because a "trade-off" occurs when a beneficial change in one trait (e.g. reproduction) is linked to a detrimental change in the other (e.g. survival; Stearns 1989). Thus, reproductive plasticity is constrained by trade-offs which occur with any change in a reproductive trait, and should evolve only in relation to its contribution to the lifetime reproductive potential of the individual (Negus and Berger 1987).

Numerous models have been employed to explain the evolution of basic reproductive patterns (e.g. iteroparity vs. semelparity) as well as "optimal" strategies which can be defined as combinations of life-history traits such as age of first reproduction, litter size and reproductive effort (see review by Stearns 1976). However, due to trade-offs, Stearns (1976) points out that there is no assurance that a species will express an optimal reproductive strategy. This is because the particular strategy developed under one environmental regime may constrain the degree to which particular traits can be optimized for a different set of conditions. That is, the evolutionary history of a species will influence its potential for reproductive plasticity, and thus its ability to adopt different strategies. Therefore, the strategy expressed by a species will be a compromise between "optimal" and available strategies.

The extent to which sea otter life-history traits are plastic, and how they may differ from theoretical "optimum" is not well defined. However, the recent history of the species provides a unique opportunity to examine the reproductive strategies of this species under a range of ecological conditions. This history began with Russian exploration of Alaska beginning in 1741. Russian and then American hunters nearly exterminated the sea otter throughout its range (Kenyon 1969). One of several remnant sea otter populations survived on Amchitka Island, Alaska. Following federal protection in 1911, the population recovered, and has remained at a presumably stable equilibrium population since the 1960's (Estes 1990). In contrast, several areas in Alaska, including



Kodiak Island, still contain unoccupied habitat with an expanding sea otter population available for study. Comparisons of areas with equilibrium and expanding sea otter populations have been used extensively to examine the effects of sea otters on the near-shore habitat they occupy (see Estes and Duggins 1995). Similar comparisons would be valuable when comparing sea otter reproductive strategies.

Jameson and Johnson (1993) concluded that no evidence presently exists to suggest a relationship between population status (and thus resource availability) and natality in wild sea otter populations, indicating little plasticity in reproductive output. However, changes in birth rates, reproductive success and adult survival may only become apparent under "stressful" conditions such as those acting within equilibrium density populations when food resources may become limiting (Reznick 1985). Early studies of sea otter reproduction used cross-sectional data (analysis of reproductive tracts of animals collected at a point in time), and are subject to interpretation based on assumptions about reproductive intervals and synchrony (Kenyon 1969, Schneider 1973). Studies using longitudinal data (observations of marked individuals through time) are free from these assumption, but have only been conducted on populations existing at unknown or below equilibrium densities (Garshelis et al. 1984, Wendell et al. 1984, Siniff and Ralls 1991, Jameson and Johnson 1993, Riedman et al. 1994, Monson and DeGange in press), and thus the full effect of resource limitations on reproduction in sea otters is not known. Furthermore no studies have attempted to reconcile sea otter life histories with predictions of life-history theory.

The objective of this study was to measure birth rates, reproductive success and adult survival in an equilibrium population of sea otters at Amchitka Island, and compare these results with similar information from an expanding sea otter population at Kodiak Island, Alaska (Monson and DeGange in press). Results show birth rates and adult female survival rates remained high in Amchitka while reproductive

success was depressed. These findings corroborate Jameson and Johnson's (1993) claim of invariant birth rates in sea otters, and indicate that population regulation in this species is under the control of factors affecting juvenile survival. However, this result appears counter intuitive. A few high quality young with a high probability of survival would seem a more reasonable strategy than producing more offspring with a low probability of survival. Thus, the sea otter's reproductive strategy is examined in light of predictions made from "bet-hedging" models of life-history theory (Stearns 1976) with consideration of the constraints of their evolutionary history.

## METHODS

## Study Area

This study was conducted at Amchitka Island, Alaska located in the Rat Island group of the western Aleutian archipelago (Fig. 1). The coast is predominantly rocky with a fairly continuous intertidal bench extending seaward from low cliffs. The canopy forming kelp *Alaria spp.* delineates a shallow rocky shelf that extends up to several kilometers from shore around much of the island. See Merritt and Fuller (1977) for a detailed physical and biological description of Amchitka. The core study area was located between Sea Otter Point and East Cape on the Bering Sea side of the Island (Fig. 2). Within this area males and females tended to segregate by sex, as described by Kenyon (1969). Crown Reefer Point (CRP) and East Cape were male aggregation sites within the study area while the intervening coast supported females and territorial males.

The green sea urchin (*Strongylocentrotus polyacanthus*) was abundant due to high, consistent recruitment (Estes and Duggins 1995). However, due to otter foraging activity, the urchin population exists at a relatively low biomass compared to non-otter-exploited urchin populations in the western Aleutians (Estes and Duggins 1995). Even so urchins were the dominant prey species of otters at Amchitka during this study (Watt *et al.* submitted). Otters also foraged on several species of bivalve mollusks, crustaceans, octopus and epibenthic fish, and the Pacific lump sucker (*Aptocyclus ventricosus*) was a particularly important supplement in winter and early spring during this study (Watt *et al.* submitted). The abundance of lump suckers appears to be a long-term episodic event, and may have created exceptional conditions with respect to food abundance for Amchitka. The result of this abundant, easily captured food resource may explain a general increase in the physical condition of sea otters captured in the second year of this study (see Mass/Length Analysis).

## Study Animals

Ninety-six sea otters were captured in July of 1992, and 22 (including 3 recaptures) were captured in August 1993 using un-weighted tangle nets, or diver operated Wilson Traps (see Ames *et al.* 1983). Thirty-four adult and 8 juvenile females, 21 adult and 5 juvenile males, and 11 dependent pups were instrumented with surgically implanted radio transmitters (Advanced Telemetry Systems, Inc., Isanti, MN). Anesthesia and surgical procedures are describe by Williams *et al.* (1981), and Williams and Siniff (1983). Each instrumented animal was marked with a unique combination of colored plastic tags (Temple Tags, Temple, TX) attached to the hind flippers (Ames *et al.* 1983). Twenty-two additional adult females were marked with flipper tags only. A premolar tooth was collected for age determination, and mass (kg), length (cm) and identifiable marks were recorded. Mass and length were both measured while the animal was anesthetized to minimize measurement error. Age at capture was estimated from decalcified longitudinal sections of the premolar tooth (see Garshelis 1984 and Pietz *et al.* 1988). Sections were prepared and read by Matson's Laboratory (Milltown, MT). Age was incremented in subsequent years based on the date of capture.

Radio instrumented otters were located using programmable scanning receivers (Advanced Telemetry Systems, Isanti, MN), and identified using binoculars and high power spotting scopes (Questar Corp. New Hope, PA). Otters marked only with flipper tags were observed opportunistically. Searches were land based (walking sections of coast and scanning at high points) or from a 17' Boston Whaler using a twin side-looking antenna array. Telemetric relocations and visual observations of marked sea otters were attempted at least weekly from July 1992 through March 1994, and once during June 1994. Data collected for each relocation included date, time, location, presence or absence of a dependent pup (for females), and evidence of mating activity including the presence of a male consort and/or a fresh nose injury (Foott 1971). Most relocations were within the core study area between Sea Otter Point and East Cape

(Fig. 2). However, several island-wide searches were conducted by boat, and road-accessible areas along the coast to Aleut Point, at the far west end of the island, were periodically checked for missing animals.

In addition to information gathered from marked individuals, surveys to determine pup/adult ratios were conducted monthly along 2 segments of coast. The Constantine Point (COP) survey area was within the core study area on the NE side of the island, and the Rifle Range Point (RRP) area was outside the core study area on the SE side of the island (Fig. 2).

Monthly beach surveys to recover sea otter carcasses were conducted at RRP and at CRP to supplement information on sea otter mortality patterns. However, most carcasses were recovered opportunistically or during island-wide carcass searches each spring.

### Analysis

Mass/length (M/L) ratios ( $\text{kg}\cdot\text{cm}^{-1}$ ) of living (and presumably healthy) otters at Amchitka were compared with M/L ratios collected in the same manner by Monson and DeGange (unpubl. data) at Kodiak Island, AK in 1986-1987. Between area comparisons of M/L ratios of young animals (1 to 4 years old) were made for males and females separately with two-factor ANOVA using study site and age as factors. Only non-pregnant, non-lactating females were used in the female comparison. T-tests were used when comparing mean mass, length and M/L ratios of adults for varying age and/or reproductive status categories. Arcsine transformation was performed on M/L ratios prior to analysis to normalize data.

Annual birth rates ( $\text{pups}\cdot\text{female}^{-1}\cdot\text{year}^{-1}$ ) were calculated in two ways using methods similar to those of Siniff and Ralls (1991). One method calculated the rate from the number of pups produced per year of observation. If a female was observed with a pup in the year she disappeared or the study ended, she was considered to have been monitored for the entire reproductive year (365 otter days), thereby

avoiding inflation of the estimated birth rate. Second, birth rates were based on the inter-birth interval (birth of one pup to birth of a second) of females which produced two or more pups. Pup birth dates were never precisely known so intervals were estimated by first determining a maximum and minimum reproductive interval for each female (Wendell et al. 1984). The estimated interval length was the minimum interval plus half the unknown period. The mean estimated interval for all females which produced two or more pups was then divided into 365 days to give an annual pupping rate.

The reproductive cycle (birth to birth) is comprised of 3 non-overlapping periods: pup dependency, a short estrous period following mother/pup separation, and gestation. Sea otters generally enter estrus and mate within days of separation from their pup (Riedman et al. 1994), and thus the interval from mother-pup separation to the birth of a new pup is a good estimate of gestation. Length of gestation and pup dependency was estimated based on maximum and minimum intervals determined from pup birth and separation dates. The interval from separation to birth was estimated as the minimum length plus half the unknown period, similar to estimates of the reproductive cycle.

Pup survival from birth to weaning was determined from the estimated dependency period. Pups associated with females <120 days were assumed to have died whereas those with dependencies >120 days were assumed to have been successfully weaned. Pups not followed to separation were excluded from the analysis of preweaning survival unless minimum dependency was >120 days, in which case they were considered to have been successfully weaned. Also, pups captured as dependents which were >10 lbs (approximately 30 days old) were excluded from the preweaning survival analysis. Beyond this age the probability of success increases (Siniff and Ralls 1991, Riedman et al. 1994), and including these pups would over estimate reproductive success. G-tests were used to examine differences in proportions of pups surviving by year and season. Only two seasons were considered, summer (April-September) and

winter (October-March). Step-wise logistic regression (SAS Institute, Cary, NC) was used to examine relationships between weaning success and female condition (M/L ratio), female age and month of birth (see Sydeman *et al.* 1991). Linear regression (SAS Institute, Cary, NC) was used to examine relationships between M/L ratio, age and length of gestation as well as the relationships between length of gestation and age or month of birth.

Birth dates of pups captured as dependents were estimated by back calculation based on mass at capture, using a maximum and minimum growth rate from Monnett *et al.* (1991). Birth dates of pups potentially born after the study ended were calculated by adding 200 days (mean gestation for this study) to the estimated weaning date of the previous pup. A G-test was used to determine if monthly birth rate differed from a uniform distribution. In addition, the mean monthly ratio of pups/adult for the COP and RRP survey areas were examined for peaks in reproductive activity. Monthly preweaning pup survival rate was determined as the percentage of pups born in a month that were known to survive to weaning age. For months where <5 pups of known outcome were observed, the preweaning survival rate was estimated by adding the pups from the prior and subsequent month and again determining the proportion surviving to weaning.

Radios had an expected transmitting life of 2 years and otters were considered potential mortalities if they disappeared <20 months from instrumentation. However, only a qualitative survival analysis was conducted due to a high rate of known radio failure (tagged otters sighted after loss of radio contact). Fisher's exact tests were used to compare total disappearance rate (all otters which lost radio contact / total instrumented), confirmed radio failure rate (confirmed failures / disappearances) and unresolved disappearance rate (disappearances - failures / total instrumented) by season and sex to estimate probable levels of mortality.

The age distribution of sea otters found dead on Amchitka beaches was used to estimate  $l_x$ ,  $d_x$  and  $q_x$  values for life-table analysis (Caughley 1966) from which a survival function was constructed. This process assumes a stable population age distribution, and a constant mortality rate within age groups. However, 0-age otters are probably underestimated by carcass data as young pups are less likely to be recovered due to their small size and the possibility of removal from beaches by scavengers (primarily rats and bald eagles *Haliaeetus leucocephalus* on Amchitka Island). This bias will result in biased  $l_x$  and  $d_x$  values for all age-classes. Therefore survival to age 1 was conservatively adjusted by setting it equal to the preweaning survival rate. Assuming all other age-classes are now represented in their true proportion, the number of 0-age otters expected in the distribution ( $n_0$ ) is calculated by first observing that:  $P_0 = 1 - (n_{1+}/N)$  where  $P_0$  is the proportion of 0-age animals (set equal to preweaning mortality rate),  $n_{1+}$  is the sum of all animals in the distribution  $\geq 1$  year old and  $N$  is the new adjusted carcass sample size. After solving for  $N$ ,  $n_0$  is calculated as  $N \cdot P_0$ . From the adjusted age distribution the cumulative proportion of carcasses up to and including those in the  $i^{\text{th}}$  age-class then serves as an estimate of the proportion of mortality by the  $i^{\text{th}}$  age-class ( $d_x$ ), the reciprocal of which is the  $l_x$  value or proportion surviving to the  $i^{\text{th}}$  age-class. From these the age-specific mortality rate  $q_x$  is estimated as the number dying between the  $i$  and  $i+1$  age-class divided by the number still alive up to the  $i^{\text{th}}$  age-class.  $q_x$  values are the best indicator of mortality patterns as they are not influenced by biases associated with the 0-age-class (Caughley 1966).

All means ( $\bar{X}$ ) are presented  $\pm$  standard errors (SE). Differences in statistical comparisons were considered significant at  $P \leq 0.05$ .



**RESULTS****Mass/Length Analysis**

Young, non-pregnant females (1 to 4 years old) captured in 1992 at Amchitka were significantly lighter for their length than same age females captured at Kodiak Island (Table 1, Fig. 3). No females >4 years old were captured in Kodiak, but using 3- and 4-year-olds as a conservative indicator, non-pregnant adult females at Kodiak were significantly larger (longer and heavier) than non-pregnant adults at Amchitka (t-test,  $P < 0.001$  for both comparisons; Table 2a). More importantly, their M/L ratios were significantly higher (t-test,  $P < 0.001$ ; Table 2a). Non-pregnant, adult females at Amchitka were, on average, 3.1 kg lighter than expected based on  $0.205\text{kg}\cdot\text{cm}^{-1} \times 124\text{cm} = 25.4\text{kg}$  vs. the observed value of  $0.180\text{kg}\cdot\text{cm}^{-1} \times 124\text{cm} = 22.3\text{kg}$ ). Only palpably pregnant females at Amchitka reached M/L ratios similar to Kodiak females, presumably due to mass gain associated with pregnancy.

The mean M/L ratio of adult, non-pregnant females at Amchitka was significantly higher in 1993 than in 1992 (t-test,  $P < 0.01$ ), and was similar to the Kodiak M/L ratio of  $0.205\text{kg}\cdot\text{cm}^{-1}$  (Table 2a). Similarly, two adult females (both >5 years old) recaptured in 1993 had gained 1.8 and 2.3 kg increasing their M/L ratios from 0.17 to  $0.19\text{kg}\cdot\text{cm}^{-1}$  and from 0.22 to  $0.24\text{kg}\cdot\text{cm}^{-1}$  respectively.

As with females, M/L ratios of young males increased with age, but in contrast with females they did not differ significantly between study sites (Table 1). Non-territorial, adult males at Kodiak were significantly larger (longer and heavier) than non-territorial males at Amchitka (t-test,  $P < 0.025$  for both comparisons) but their M/L ratios were not significantly different (t-test,  $P = 0.1$ ; Table 2a). At Amchitka territorial males tended to have higher M/L ratios than non-territorial males but the observed difference was not significant (t-test,  $P > 0.2$ ). One 5-year-old adult male was re-captured in 1993, and he gained 3.2 kg over the interim and increased his M/L ratio from 0.22 to  $0.24\text{kg}\cdot\text{cm}^{-1}$ . No other males were captured in 1993.

## Reproduction

### *Annual Birth Rates and Reproductive Success*

Fifty females were observed with a total of 81 pups during the period of study, including 22 pups captured as dependents. Another 5 pups were assumed lost based on evidence of pregnancy though no pup was observed. Table 3 indicates the number of "otter days" of observation and the number of pups used to calculate birth rates and success.

Observed annual birth rates ( $\# \text{females reproducing} \cdot \text{year}^{-1}$ ) were 0.37 for 2- to 3-year-old's, and averaged 0.83 for all females  $\geq 4$  years old (fig.3). The mean inter-birth interval (pup birth to pup birth) was  $341 \pm 12.7$  days ( $n=31$ ) corresponding to an average annual birth rate of 1.07 (Table 4). Females that lost a pup soon after parturition generally did not delay in having another pup, and had a mean inter-birth interval of only  $263 \pm 14.8$  days ( $n=11$ ; Table 4). The mean inter-birth interval for females who successfully weaned pups was  $383 \pm 8.1$  days ( $n=20$ ) for an average annual birth rate of 0.95.

Mean length of dependency for successfully weaned pups was  $180 \pm 5.2$  days ( $n=37$ ; Table 4). Generally, females which lost pups did so within two months of parturition, and had a mean dependency period of  $40 \pm 7.8$  days ( $n=23$ ; Table 4, Fig. 5). Ten pups had estimated dependency periods of between 90 and 150 days which are of questionable outcome. Of these, 4 had dependencies  $< 120$  days and were considered unsuccessful where as 6 had dependencies  $> 120$  days and were considered successful.

Reproductive success (defined as  $\# \text{pups surviving to} \geq 120$  days  $\cdot$  total pups produced<sup>-1</sup>) was 0.14 for 2- to 3-year-old's, and was 0.56 for 4- to 12-year-old females, but dropped to 0.20 for females  $> 12$  years old (Fig. 4). Success in year  $t$  was not correlated with success in year  $t-1$ . Five of 10 females who successfully weaned pups in the first year were successful the following year, and 6 of 12 who were unsuccessful in the first year were successful the following year. Five and 6 females were successful and unsuccessful in 2 consecutive years respectively.

Reproductive success was positively correlated with M/L ratio of the female (Fig. 6) but the relationship could not be shown to be significant (Logistic regression,  $P = 0.07$ ). The proportion of pups that survived to weaning was significantly higher for those born in summer (0.65,  $n=31$ ) than in winter (0.20,  $n=20$ ; Fisher's exact,  $P < 0.004$ ). Pups born between October and January had the lowest probability of survival (0.11,  $n = 9$ ; Fig. 7).

Because females had significantly higher M/L ratios in 1993, first and second year weaning success was examined. Only summer and fall data were comparable. Birth rates were 0.80 and 0.85 for 1992 and 1993 respectively while success was 0.29 ( $n = 7$ ) in 1992 compared with 0.54 ( $n = 13$ ) in 1993. These could not be shown to be different (Fisher's exact  $P = 0.38$ ) although small sample sizes resulted in a fairly low power test ( $\beta=0.18$  at  $\alpha=0.05$ ).

#### *Gestation and Reproductive Synchrony*

Mean length of gestation was  $200 \pm 3.7$  days ( $n=37$ ; Table 4), and showed no relationship with female age, length of her previous pup's dependency period or month of conception. However, three females delayed or extended gestation by approximately 100 days with a mean apparent gestation of  $309 \pm 5.4$  days (Table 4, Fig. 8). Seven additional adult females had not been observed with a pup for periods ranging from 250 days to  $>1$  year before they were no longer seen or the study ended.

Pups were born in every month of the year, but monthly pupping rates had a broad seasonal peak centered in May (Fig. 7). The seasonal distribution of births was significantly different from uniform (G-test,  $P < 0.001$ ). Monthly surveys confirmed the late spring pupping peak in the general population (Fig. 9). The broad pupping peak gave rise to a similar peak in mother/pup separations and subsequent mating centered in October (Fig. 10).

## Survival

Several pre-mature radio failures were confirmed by re-sightings of tagged individuals following disappearance of their radio signals. Confirmed failures occurred at a relatively steady rate and were distributed equally throughout the year with 9 occurring in the winter months and 11 occurring in the summer months (Table 5). No significant differences could be found in the total disappearance rate between females and males, or between adults and young animals (Fisher's exact,  $P > 0.1$  for all comparisons; Table 6). Females who disappeared tended to be resighted, thus confirming radio failure, more often than males (0.54,  $n=24$  vs. 0.33,  $n=21$ ; Fisher's exact,  $P = 0.2$ ). Thus, compared with females, males had a significantly higher rate of unresolved disappearances which represent potential mortalities (0.45,  $n=31$  vs. 0.22,  $n=49$ , Fisher's exact,  $P = 0.05$ ; Table 6). In addition, unresolved disappearances occurred significantly more often during winter than summer compared with confirmed failures (0.76,  $n=25$  vs. 0.45,  $n=20$  respectively; Fisher's exact,  $P=0.03$ ; Table 5), primarily because of the high disappearance rates of males and weanlings in winter (0.90,  $n=10$  and 0.75,  $n=8$  respectively). Three of 4 known mortalities also occurred during winter months.

No dependent pups instrumented in the summer of 1992 ( $n=6$ ) were known to be alive by June 1993, but 2 of 5 pups radio instrumented in 1993 were still alive in June 1994 (Table 7). Both of these were female. None of the missing pups (or adults) were located during periodic island-wide searches.

Beach surveys recovered very few fresh sea otter remains. A total of 13 of 156 carcasses (8.3%) were relatively fresh. Most remains (89%) were old weathered bones, and often involved only the skull (76%). The age distribution of sea otters found dead during beach walks at Amchitka was comprised of 39% young (<2 years old), 18% prime (2-8 years old), and 43% old (>8 years old) age-class animals (Fig. 11). After correcting survival to 1 year of age, the estimated survival ( $L_x$ ) and

mortality ( $q_x$ ) functions for sea otters at Amchitka were determined (Fig. 12). These curves indicate mortality drops substantially after the first year, and is low from age 1 to about 4 or 5 years of age when it slowly begins to increase. Mortality then begins to increase more rapidly after approximately 8 or 9 years of age. However, 8-year-old and 13-year-old otters appeared to be under-represented in the age distribution resulting in drops in the observed mortality rate for these age-class otters.

## DISCUSSION

## Demography of an Equilibrium Sea Otter Population

*Population Condition*

The sea otter population at Amchitka Island has been thought to exist at equilibrium densities for several decades (Kenyon 1969, Estes 1990). In contrast, the Kodiak study examined an expanding population with abundant resources (Kvitek *et al.* 1992, Doroff and DeGange 1994), and thus served as a reference to determine relative condition of the Amchitka population.

The low M/L ratios of female sea otters at Amchitka in the first year of the study (Fig. 3, tables 1 and 2) is consistent with the idea that the population was resource limited. However, females appeared more severely affected by resource limitations than both territorial and non-territorial males (Table 1 and 2). Territorial males presumably live in the highest quality habitat (thus attracting females), and are also capable of stealing food from adult females feeding within their territory (Riedman unpubl. ms., Watt unpubl. ms.). Thus, their high M/L ratios are not surprising. However, non-territorial males are relegated to "male areas" (Kenyon 1969) which are generally more exposed, and expected to represent inferior quality habitat in an equilibrium population (thus not utilized by adult females). The relatively high M/L ratio of non-territorial males did not support the hypothesis that "male areas" in equilibrium populations are necessarily of lower quality in terms of food resources. A similar pattern was observed by Kenyon (1969) when he compared mass and lengths of otters at Amchitka with those from a still expanding population off the Alaska Peninsula (Table 2b). However, in his comparison adult males as well as females at Amchitka appeared to have depressed M/L ratios.

The higher M/L ratios of adult females at Amchitka in the second year (Table 2a) indicate that the episodic appearance of Pacific lump sucker (Watt *et al.* submitted) subsidized the prey resource base for sea otters, and thus improved the general condition of the population. In

comparison to earlier studies (Kenyon 1969, Estes 1977) few fresh carcasses were recovered in winter and spring further indicating that conditions were relatively favorable during this study.

### *Annual Birth Rates*

Sea otters at Amchitka generally did not delay reproductive attempts (Fig. 8), or experience significant reductions in fecundity rates relative to growing populations (Fig. 4). However, the estimated annual birth rate of 0.83 (based on pups•#otter yrs<sup>-1</sup> for adults ≥4 years old) is the lowest for a sea otter population to date. Other estimates range upwards of 0.88 (Siniff and Ralls 1991, Bodkin et al. 1993, Jameson and Johnson 1993, Riedman et al. 1994, Monson and DeGange in press). However, early pup mortality (Fig. 5) likely resulted in unobserved pup births. In contrast, the estimated annual birth rate of 0.95 - 1.07 based on mean inter-birth interval (Table 4) is similar to estimates from other studies. The interval method may tend to over estimate birth rates in short term studies such as this (Eberhardt and Schneider 1994). This is because females not observed with pups for extended periods will not contribute to the estimate if they are never seen with more than one pup during the period of study. Alternatively, some long inter-birth intervals may represent unobserved pup births, implying the estimate based on inter-birth interval is more appropriate.

### *Reproductive Intervals*

We might expect reproductive intervals to be more variable and possibly longer in a equilibrium population assuming limited resources cause slow pup growth, and/or periods of reproductive inactivity or failure (Garshelis et al. 1984). However, reproductive intervals at Amchitka (Table 4) were similar when compared with other studies (Wendell et al. 1984, Siniff and Ralls 1991, Jameson and Johnson 1993, Riedman et al. 1994, Monson and DeGange in press). Gestation varied ±50 days around a mean of near 200 days for all studies and was not

correlated with female age, condition, length of previous dependency, or month of conception in this study. Some variation is due to error in estimates as actual breeding dates and birth dates are rarely known. It may be related to individual female differences (i.e. some females tend to have longer or shorter than average gestation) but insufficient data were collected in this study to examine this hypothesis.

It is unclear if the females which appeared to delay reproduction failed to conceive for a period of time, or had extended gestation by lengthening the period of delayed implantation. Two of 3 gestation periods >100 days of the mean (Table 4, Fig. 8) resulted in moving parturition from a time of low probability of success (February) to a time of higher probability of success (May) suggesting a lengthening of gestation to adjust timing of birth. However, this may have been coincidental as only 2 of 12 gestation periods between  $\pm 30$  to  $\pm 50$  days of the mean moved parturition in the direction of the seasonal pupping peak. Thus, gestation length did not appear related to reproductive synchronization. In addition, Riedman *et al.* (1994) found some females mated several times at intervals of up to 3 months before successfully reproducing, indicating the 3 with gestation periods >100 of the mean likely failed to conceive at least once and subsequently mated successfully. Brosseau *et al.* (1975) found captive otters cycled at approximately 5 week intervals when not breeding thus indicating 2 unsuccessful mating periods occurred in my study.

Some females were not observed with pups for periods as long as a year, and may have had and lost a pup which was not detected or skipped a reproductive event. Five females showed signs of having been pregnant but were not observed with pups, and thus they were assumed lost. Others were simply not observed with pups for extended periods. Females with extended pupping intervals tended to have lower M/L ratios than females with regular pupping intervals ( $0.173 \pm 0.004 \text{kg} \cdot \text{cm}^{-1}$ ,  $n=8$  vs.  $0.186 \pm 0.003 \text{kg} \cdot \text{cm}^{-1}$ ,  $n=33$ ;  $t$ -test,  $P = 0.067$ ). Physical condition is an important factor in conception rates of mammals (Albon *et al.* 1983,



Bronson 1989, Wauter and Dhondt 1989). Thus, some of these females may have failed to conceive for extended periods or experienced reproductive failure. However, M/L ratio appears to influence reproductive success (Fig. 6), and undetected pup loss is an equally likely explanation.

Mean successful pup dependency at Amchitka was 180 days and ranged up to 260 days (Table 4), and is similar to dependencies in California where two studies found a mean of 189 and 166 days with maximums near 290 days for both (Siniff and Ralls 1991 and Riedman *et al.* 1994 respectively). Dependencies averaged 170 days and ranged up to 330 days in Prince William Sound, Alaska (Monnett *et al.* 1991). Mean successful dependency on Kodiak Island, Alaska was significantly shorter (t-test,  $P < .05$ ), and was only 153 days with a maximum of 210 days (Monson and DeGange in press). However, variability tended to increase with sample size. Kodiak had the smallest sample size, and only 10 dependencies were followed to separation. Several older pups in the Kodiak study were past minimum weaning age but not followed to separation so the full range may not have been observed. In general, the data do not support the hypothesis that dependency increases in variability in an equilibrium population in comparison to growing populations. However, this observation does not preclude other changes occurring such as an increase in minimum successful weaning age or reduced weaning mass due to slower pup growth rates in an equilibrium population. Interestingly M/L ratios of yearlings are similar between Kodiak and Amchitka (Fig. 3).

Even considering the above delays and possible reproductive failures, average annual birth rates were very similar to those estimated from other studies under a wide range of conditions. In part, this was due to the lack of delayed reproduction when pups were prematurely lost. Unsuccessful females had a mean inter-birth interval of only 263 days which translates to an annual birth rate of 1.39 (Table 4) thus compensating for the potentially reduced reproductive activity for some animals. These results corroborate the estimated birth rates

for Amchitka of between 0.80 to 0.90 (Jameson and Johnson 1993) obtained by reanalysis of reproductive tract data collected by Kenyon (1969) and Schneider (1973), and support Jameson and Johnson's (1993) earlier conclusion of invariant birth rates in relationship to population status for this species.

### *Reproductive Success and Adult Survival*

Equilibrium populations must balance mortality with reproduction. Overall, 24 of 51 pups (47%) survived to the minimum weaning age at Amchitka in comparison with up to 22 of 26 (85%) surviving at Kodiak (Monson and DeGange in press; Fig. 4, Fisher's exact,  $P < 0.002$ ). Thus success at Amchitka is as low as any estimate for a sea otter population to date (Siniff and Ralls 1991, Jameson and Johnson 1993, Riedman et al. 1994). This result is even more compelling when considering that Siniff and Ralls (1991) and Jameson and Johnson (1993) used 150 days as minimum weaning age while I used 120 days based on findings from Riedman et al. (1994). If 150 days is, in fact, a better estimate of minimum weaning age for Amchitka pups then success during this study may have been as low as 35% (18 of 51). Conversely, if 120 days is a better minimum for California then those studies using 150 days as a minimum under estimated preweaning survival. Assuming mass and length measurements on shot animals are comparable with those of drugged animals the M/L ratios of females during the early 60's (Kenyon 1969) may have been lower than during this study (Table 2b), and thus preweaning success also may have been lower in the early 1960's (Fig. 6). Results of stepwise logistic linear regression indicate preweaning mortality was most related to age and M/L ratio (although these two factors are related), and secondly by month of birth.

In contrast, prime-age survival rates at Amchitka did not appear depressed (Fig. 12). Annual survival rate estimates of adult females range from >90% in California (Siniff and Ralls 1991) and at Kodiak Island (Monson and DeGange in press). The age distribution of otters

found dead during this study contained 18% prime-age animals (Fig. 11), and was similar to the age distribution found by Ancel Johnson in Prince William Sound, Alaska where 17% were prime-age (Monson et al. 1994). In contrast weanling survival to 1 year old at Amchitka was relatively low (Table 5, 6 and 7) although dispersal of radio-instrumented weanlings could not be conclusively ruled out. Male pups, in particular, are more likely to disperse (Garshelis et al. 1984). However, no missing otters were located on island wide searches suggesting dispersal was not the sole reason for the high disappearance rate in my study. Kenyon (1969) found the majority of mortalities were juveniles or animals showing signs of advanced age. Thus survival after 1 year of age appears to be maintained at high levels (at least in unperturbed populations) before beginning to decrease again in older age-classes (Fig. 12). This is a typical mortality pattern for long-lived mammals (Caughley 1966, Emlen 1970, Siler 1979).

#### *Implications for Sea Otter Biology*

These results are evidence that sea otters exhibit little plasticity in reproductive output, and that population regulation occurs primarily through mechanisms affecting survival from birth to 1 year of age. Thus, relatively large numbers of reproductively mature females remain in the population even during periods of severely limited resources, low recruitment and generally high mortality. When favorable conditions occur the population can respond relatively rapidly by increasing recruitment. This mechanism of population regulation implies that an equilibrium population may increase and decline with long term fluctuations in the environment. This also implies that a stable age distribution in equilibrium populations may not exist. For example, the relative paucity of 8 year old animals in the age-distribution (Fig. 11) has two possible origins. Either it is an artifact of the aging technique due to some unknown bias against assigning a certain age to teeth, or it may be due a real lack of animals in that age-class due to

a particular poor year of recruitment. The aging technique is known to contain error, however no biases have been observed in studies of known age teeth (Bodkin pers. com.) and thus there is no reason to suspect that the absence of 8-year-olds in my sample is a methodological bias. Rather, it may be due to an episodic cohort failure. The age distribution of sea otters in Prince William Sound also suggests cohort failures (Udevitz pers. com.).

### Reconciliation of Reproductive Strategies

The reproductive patterns in sea otters seems counter intuitive from an energetics perspective. Why produce pups that have little chance to survive? As pointed out by Schaffer (1974b), lower survival among the immature age-class is equivalent to a reduction in per unit fecundity, and thus selection should favor reduced reproductive output. Thus, for organisms like sea otters, trade-offs might occur which favor reproduction even when the potential for success is low. Conversely, there may be no selective advantage in delaying reproductive events, as imagined for organisms that "bet-hedge" (Stearns 1976).

Bet-hedging may occur for organisms that reproduce in the face of uncertainty. In contrast to the concept that a few high quality young are preferable to many low-quality young, a bet hedger will produce just a few more young in order to take advantage of unpredictable fluctuations in conditions (Stearns 1976). The result is a net advantage in the number of surviving young. Galapagos fur seals (*Arctocephalus galapagoensis*) are an excellent example of bet-hedgers. Unlike most pinnipeds, pups of this species are dependent and nurse until 2 or 3 years of age (Trillmich 1984). However, they mate each year even though the presence of a suckling 1-year old sibling always results in the death of the newborn. This strategy insures that an adult female will be pregnant and produce a pup the next year if they prematurely loose the prior year's pup, which occurs in about 20% of cases. Also, 50% of pups born while a female is nursing a two-year-old

survive resulting in a net increase in reproductive potential by allowing dependencies up to 3 years while still successfully reproducing every 2 years.

Bet-hedging models predict that, for a species living in a fluctuating environment in which adult survival is high and invariant relative to juvenile survival, the optimal strategy is: 1) iteroparity, 2) late maturation and long life spans, 3) more and smaller litters, and 4) low reproductive effort (Schaffer 1974a, Wilbur et al. 1974, Goodman 1979, Stearns 1976). Reproductive effort is the amount of energy provided to off-spring relative to maternal maintenance costs. One aspect of low reproductive effort was termed reproductive "restraint" by Curio (1983), and is defined as the parent providing less to its offspring than is physiologically possible in order to ensure its own survival and subsequent reproductive success. That is, to maximize reproductive potential, an individual must also minimize the probability of leaving no young at all (Stearns 1976). Under the conditions of the model, maximizing life span and the number of offspring produced is favored over the success of one particular reproductive attempt.

Several reproductive traits of sea otters match these predictions quite well. Age of first reproduction is 2 to 5 years and females produce pups until they are quite old (up to 20 years Riedman and Estes 1990). Thus, relative to many mammalian species, they are long lived and mature late in life. Litter size is limited to one for each reproductive attempt (Kenyon 1969) even under ideal conditions. Thus litter size is unarguably "small". However, they have non-overlapping gestation and lactation, relatively long gestation periods due to delayed implantation (Sinha et al. 1966), and relatively long periods of dependency requiring extensive maternal care which appear counter to predictions of "more" reproductive attempts and relatively low reproductive effort. These apparently contradictory observations from the ideal bet hedger may be due the constraints of their evolutionary history. From this perspective we can ask if sea otters reproduce

optimally given the options available to them, or if it is simply their only available option?

### *Litter Size*

Constraints induced by the evolutionary history of the species no doubt have had an effect on the sea otter's reproductive strategy. Litter size is limited to one per reproductive event. Even though this is in agreement with a predicted "small" litter size there is no reason to believe it is the optimal number for an animal of this size under these conditions. Alternatively, they do not have the option to increase litter size. Females carry newborn pups on their chest to insulate them from the cold ocean environment, and the large energetic demands of care and feeding preclude successfully raising more than a single young. This is evident by the fact that twins, though occasionally observed in this species invariably result in the death of at least one sibling (Kenyon 1969, Schneider 1973, Williams et al. 1980, Jameson and Bodkin 1986). In addition, due to the harsh conditions into which newborn pups are born they must be relatively large and well developed at birth if they are to survive (Millar 1977). As fetal mass may be limiting, selection will favor one very large pup rather than a number of smaller off-spring. In fact, based on the relationship between mean adult mass and birth mass determined for terrestrial mammals by Millar (1977), newborn sea otters are 3 to 4 times larger than expected. The birth mass of sea otters is about 2kg (Kenyon 1969, Monnett et al. 1991) whereas the predicted birth mass, based on the average female mass at Amchitka Island, is about 600g. This may be a general marine adaptation as a single, relatively large pup is common to all marine mammals (Estes 1979, Estes 1989). In contrast, most terrestrial mustelids have litters of several small pups born in dens which protect and insulate them from the environment.

### *Lifetime Reproductive Potential*

Mutually exclusive periods of pregnancy and lactation limits the potential number of lifetime reproductive attempts in the sea otter. Because the average length of successful is dependency less than gestation, concurrent pregnancy and lactation could reduce the inter-birth interval, thus substantially increasing life-time reproductive potential. When gestation and dependency are relatively short and strong seasonal constraints favor annual reproduction, concurrent reproductive states confer little advantage, and separate gestation and lactation periods might be expected. This is generally true of mustelids which have short gestation periods, and the entire reproductive cycle occurs within the summer season. In contrast, the fisher (*Martes martes*) has a post-partum estrus within days of parturition (Asdell 1946), and the wolverine (*Gulo gulo*) may mate within a few months of parturition while still with dependent young. Both have relatively long gestation periods of approximately 350 days and 270 days respectively (Mead 1981).

Sequential pregnancy and lactation is a common mammalian strategy that separates the energy requirements of the two periods although the period of delayed implantation in sea otters results in almost no energy expense in early gestation. However, the energy requirements of lactation in the sea otter may be extreme due to their high metabolic rates (Costa and Kooyman 1982), and though pregnancy is relatively inexpensive energetically (Millar 1977) it may be that sea otters are unable to withstand any additional expense. Alternatively separation of these periods may be favored by providing an approximately annual reproductive cycle which would result in maintaining pupping at favorable times of the year (see Reproductive Synchrony). It would also provide longer recovery time between late lactation and the birth of a new pup. This may allow energy stores to be replenished prior to parturition, thus increasing the success probability of the subsequent pregnancy. A third alternative may be that behavioral constraints

prevent successful mating behavior to occur while females are accompanied by dependent young (Kenyon 1969).

The 2 to 3 month period of delayed implantation further lengthens the reproductive cycle. Although all mustelids are physiologically capable of delayed implantation, it is not universally expressed (Weir and Rowlands 1973). Many mustelids have relatively long periods of unimplanted pregnancy (e.g. river otter *Lutra canadensis*, badger *Taxidea taxus*, marten *Martes spp.*, stoat *Mustela erminea* and wolverine *Gulo gulo*) while others exhibit no delay (e.g. Eurasian otter *Lutra lutra*, ferret *Mustela putorius*, and least weasel *Mustela nivalis*; Mead 1981). This character even varies within species as the western form of the spotted skunk (*Spilogale putorius latirons*) exhibits extended periods of delayed implantation while the eastern form (*Spilogale putorius ambarvalis*) does not (Mead 1981). Thus it would appear that the sea otter would have a "choice" in the use of delayed implantation. It has been suggested that the length of the unimplanted period in sea otters may depend on external stimuli or the condition of the individual (Brosseau et al. 1975). I did not find evidence of season (see reproductive synchrony) or condition affecting length of gestation periods in this study. Alternatively, it may be favored by providing annual inter-birth intervals and longer recovery periods between births. Both explanations may be important as if only energy storage were important, sea otters in expanding populations would be expected to shorten the length of gestation because relatively less time should be required to replenish losses incurred in rearing a pup. Although we have limited data on length of gestation from Kodiak, there is no evidence that it is shorter than Amchitka (218  $\pm$ 14 days in Kodiak vs. 200  $\pm$ 4 days at Amchitka). Conversely if only annual cycle length were important, sea otters in equilibrium populations may be expected to shorten gestation thus providing time for longer dependency periods which could increase weanling survival. Again, the consistent length of reproductive intervals between various studies does not support this.



### *Reproductive Synchronization*

Peaks in sea otter reproductive activity have been observed in many studies including this one (Fig. 7 and 9; Kenyon 1969, Monnett *et al.* 1991, Siniff and Ralls 1991, Jameson and Johnson 1993) while not in others (Riedman *et al.* 1994, Monson and DeGange *in press*). However, the mechanism of synchronization has not been examined. Jameson and Johnson (1993) speculated that, because sea otters have delayed implantation, synchronous reproduction should result from adjustments linked to environmental cues such as photoperiod. This is a common pattern in delayed implantation (Weir and Rowlands 1973), and a strategy used by many mustelids (particularly those with extended periods of unimplanted pregnancy) (Canivenc and Bonnin 1981, Mead 1981) and by pinnipeds (Boyd 1991). However, sea otters in this study did not delay reproductive attempts or adjust the length of gestation resulting in pups births during the seemingly unfavorable winter months (Table 4, Fig. 7 and 8).

Negus and Berger (1987) suggest that when the scale of temporal uncertainty exceeds a species generation time, then environmental cues such as photoperiod contain no useful information and continuous breeding is favored. This would be consistent with bet-hedging theory as we would not expect delays between reproductive attempts to take advantage of favorable conditions when they occur. Even though peaks in reproduction occur, sea otters are continuous breeders.

An alternate explanation for the synchrony seen in the Amchitka population assumes that gestation is relatively fixed (providing an annual reproductive cycle and some recovery time between pups), and the probability of survival for pups born from October to January is consistently low (Fig. 7). Loss of a pup during these months (Fig. 10) translates to the birth of the subsequent pup approximately 200 days later during the April to August peak. The relatively high success rates for pups born during these months (0.65; Fig. 7) and the annual nature of a successful reproductive cycle ( $\bar{X}$  = 383 days; Table 4) would serve to maintain this peak. Thus otters at Amchitka did not appear to

synchronize reproduction in response to environmental cues. Instead otters "hedged their bets" and reproduced without delay even when pups were born in winter. This strategy would be favored by a bet-hedger because a failure in winter would synchronize the birth of the subsequent pup with the more favorable summer period, and a success would increase the individual's net life-time reproductive success.

The fact that sea otters at Amchitka did not use delayed implantation to synchronize births with the more favorable period suggests the advantages of bet-hedging outweigh the advantages of always synchronizing reproduction with the seasonal optimum. Siniff and Ralls (1991) also found female sea otters did not delay reproductive attempts, and observed a second birth peak linked to an earlier period of high pup mortality in the southern portion of the California range. Riedman et al. (1994) found no pupping peak in the more protected Monterey Bay, California population. Similarly, sea otters on Kodiak exhibited only a weak or no seasonal peak in reproduction presumably due to relatively uniform monthly pup survival (Monson and DeGange in press). The Prince William Sound, Alaska, sea otter population exhibits a very distinct seasonal peak in pupping (Monnett et al. 1991), and occupies the most northerly habitat of any population. It is not known if the peak in pupping in Prince William Sound is due to pup mortality patterns or results from the stronger seasonal cues affecting this population. However, in general, it does not appear that reproduction in sea otter populations is synchronized by physiological mechanisms.

#### *Reproductive Effort*

Bet-hedging implies that if reproductive failure is imminent, it should occur prior expenditure of significant amounts of energy in a reproductive attempt. For mammals, where lactation is energetically expensive relative to mating and gestation (Millar 1977), this would mean losses should occur prior to or soon after parturition. This strategy is evident in the Galapagos fur seal. Although all females

mate each year, only 15% of females with dependent pups actually give birth the following year compared with 70% without pups (Trillmich 1984). This indicates that pregnancy generally fails if lactation is maintained. However, when pups are born to females suckling older pups, the newborn usually dies within a month of birth (Trillmich 1984).

Sea otters have metabolic rates 2.5 - 3.0 times higher than those of terrestrial mammals of similar size (Costa and Kooyman 1982) and thus the cost of lactation may be particularly high. In addition, sea otters have little capacity to store energy, and thus they must contend with the energetic cost of lactation and pup care with the resources immediately available. To compound their energy problems, females with newborn pups spend less time feeding and more time resting and grooming their pups than they do with older pups or when alone (Gellet pers. com.). Reproductive failures occur soon after parturition (fig 5; Siniff and Ralls 1991, Riedman et al. 1994, Monson and DeGange in press) indicating early lactation is crucial to pup survival. Reproductive success in this study also appears to be linked with condition of the female (Fig. 6). These observations suggest that female sea otters at Amchitka Island that did not possess sufficient energy stores at parturition were not able to reduce foraging activities sufficiently to care for a pup without risking her own survival. This is also the definition of reproductive "restraint" which bet-hedging theory predicts.

The energetics of sea otter reproduction may also favor bet-hedging in sea otters. If sea otters can not store significant amounts of fat then delaying the interval between pup separation and birth (beyond that fixed by the length of gestation) may not increase condition significantly and thus be of little selective value. This seems likely because an added benefit of bet-hedging, if it fails, is to synchronize the subsequent birth with normally favorable conditions (figure 9).

Young sea otters may be affected by a process other than "restraint". The increase in reproductive success with age (Fig. 4; Riedman et al. 1994) suggests that young breeders may be "constrained" by lack of experience or the acquisition of skills needed for success (Curio 1983). M/L ratios increased with age in this study, and both were related to weaning success. Thus, young animals could be constrained by lack of efficient foraging skills resulting low M/L ratios and low reproductive success. Conversely, young animals have low M/L ratios resulting in reproductive restraint. These factors are confounding and difficult to separate, but likely contribute to reproductive success, as was suggested for the long-lived wandering albatross *Diomedea exulans* (Weimerskirch 1992).

Life-history theory also predicts that reproductive effort should increase with age as residual reproductive value decreases (Pianka and Parker 1975, Curio 1983, Weimerskirch 1992). This implies that reproductive success should increase with age. The expected relationship was true to a point. However, reproductive success declined in very old animals (Fig. 4), a pattern previously unreported for the sea otter. Similar results have been reported for red deer (Clutton-Brock 1984) and elephant seals (Sydeman et al. 1991). Schaffer (1974b) suggests that reproductive effort beyond a certain age should not respond to selection and either remains constant or declines. In addition, actual energetic effort is difficult to measure and decreased success does not prove decreased effort (Clutton-Brock 1984). Thus, I lack the necessary data to measure reproductive effort in the oldest age-class.

#### **Potential Limitations of This Study**

Direct statistical comparisons in this study were with only one other sea otter population studied by Monson and DeGange (in press). These are distinct populations living in very different habitats. Thus, my assessment of the influence of population status on life history

variation is pseudoreplicated (Hurlbert 1984). However, the consistency of many of my results with the findings of other studies suggest the interpretations regarding bet-hedging and optimal reproductive traits in sea otters presented here are credible. Additional comparative studies within the same habitat type with varying lengths of sea otter occupancy are needed to confirm these interpretations.

Secondly, the increased mass/length ratios of females in the second year of the study limited my ability to accurately determine the relationship between reproductive success and female condition. Mass/length ratios used to examine relationships with reproductive success were only collected at the time of capture while pups may have been born >1 year later. This would most likely decrease the power to detect a significant relationship with reproductive success. Even so the relationship presented seems plausible and represents an area needing further attention.

## CONCLUSION

Comparisons of M/L ratios indicate that in 1992 female otters in Amchitka were in relatively poor condition in comparison with females at Kodiak Island. However, this was not true of males indicating non-territorial males may not necessarily be relegated to poor quality habitat relative to food resources. Birth rates during this study were similar to estimates from Kodiak as well as other published studies, and maturity did not appear to be delayed at Amchitka. In addition, reproductive intervals were similar to intervals measured in other areas of Alaska as well as California, and delays between reproductive attempts were no more common than in other studies. Reproductive success was significantly lower at Amchitka compared to Kodiak indicating population regulation is under the control of factors affecting pup survival. Success also appeared to decline in old age which has not been reported previously for this species. Reproductive success appeared most affected by age and condition of female as well as season of birth. Pupping occurred in every month but peaked in May and June. Pups born in October - December were the least likely to survive while pups born in summer were the most likely to survive. This pattern along with the annual nature of successful reproductive attempts appeared to be the mechanism for reproductive synchronization in this population. Adult survival appeared to remain high in this equilibrium population (particularly for females).

Sea otters appear to express a reproductive strategy consistent with the predictions of "bet-hedging" models of life-history theory although constraints of their evolutionary history and energetic demands appear to make them less efficient than might be expected. However, within these constraints, the lack of plasticity in birth rates and reproductive intervals under varying environmental conditions appears adaptive for maximizing lifetime reproductive potential. Within this framework survival and future fecundity costs of reproduction are minimized at the expense of the success of individual offspring. This

maximizes female survival and consequently lifetime reproductive attempts.

Continuous reproduction in this species suggests the temporal uncertainty of environmental conditions normally exceeds the generation time for sea otters. "Bet-hedging" females continue reproducing at high rates to take advantage of favorable or at least suitable conditions when they occur, thus avoiding delays between births and increasing the number of lifetime reproductive attempts.

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Table 1. Two-way ANOVA comparing capture location and sea otter age with mass/length ratios of young sea otters (1 to 4 years old). Data collected from 1986 to 1987 at Kodiak Island, Alaska (Monson and DeGange in press), and in 1992 at Amchitka Island, Alaska.

Source	df	mass/length <sup>1</sup>	
		F	P
<b>Females</b>			
location	1	23.50	<0.001
age	3	13.92	<0.001
loc. x age	3	2.56	0.07
<b>Males</b>			
location	1	1.94	0.20
age	3	5.35	0.01
loc. x age	2	0.91	0.40

<sup>1</sup>Arcsine transformation performed prior to analysis.

Table 2a. Mean mass, lengths and mass/length ratios of sea otters captured at Kodiak Island, Alaska in 1986 and 1987 (expanding population), and at Amchitka Island, Alaska in 1992 and 1993 (equilibrium population).

Area - sex / age, status	n	$\bar{x}$	mass/length <sup>1</sup> (SE)	$\bar{x}$	mass (SE)	$\bar{x}$	length (SE)
<b>FEMALES</b>							
Kodiak '86 - '87							
3-4 yrs, non-pregnant	6	0.205A**	0.007	26.2C**,E	1.05	128F**	1.20
Amchitka '92							
>4 yrs, non-pregnant	27	0.180A**,B*	0.002	22.3C**,D*	0.34	124F**	0.70
>4 yrs, palpably preg.	10	0.216	0.008	26.8	1.12	124	0.71
Amchitka '93							
>4 yrs, non-pregnant	8	0.204B*	0.007	25.1D*,E	1.11	123	1.23
<b>MALES</b>							
Kodiak 86-87							
>4 yrs, non-territorial	7	0.250G	0.008	34.6I*	1.16	138K*	1.42
Amchitka 92							
>4 yrs, non-territorial	9	0.232G,H	0.007	31.0I*,J	0.97	134K*	1.01
>4 yrs, territorial	8	0.244H	0.007	32.5J	0.77	134	2.04

<sup>1</sup>Arcsine transformation performed on M/L ratio data prior to analysis.

\* = P < 0.05 and \*\* = P < 0.01 in paired t-test.



Table 2b. Mean mass, lengths and mass/length ratios (from Kenyon 1969) of sea otters killed in the Shumagin Islands, Alaska in 1960 (expanding population), and at Amchitka Island, Alaska from 1959 to 1963 (equilibrium population).

Area - sex / age, status	n	mass/length <sup>1</sup> $\bar{X}$	(SE)	mass $\bar{X}$	(SE)	length $\bar{X}$	(SE)
Amchitka '59 - '63							
all females	254	0.169	--	21.1	0.14	125.2	0.30
all males	79	0.210	--	28.3	0.89	135.0	0.48
Shumagin Islands '60							
all females	4	0.194	--	25.2	6.50	129.8	3.15
all males	5	0.281	--	39.5	4.53	140.8	0.22

<sup>1</sup>Arcsine transformation performed prior to analysis of M/L ratio data.

Table 3. Number of "otter days" observed and pups born to female sea otters at Amchitka Island, Alaska from July 1992 to June 1994.

Female age at birth of pup	total pups produced <sup>1</sup>	# pups excluded <sup>2</sup>	# pups successfully weaned <sup>3</sup>	# pups prematurely lost <sup>3</sup>	# otter days
2 - 3	8	1	1	6	7837
4 - 6	31	15	9	7	13864
7 - 9	17	9	4	4	6834
10 - 12	24	9	9	6	10731
<u>13 - 15</u>	<u>6</u>	<u>1</u>	<u>1</u>	<u>4</u>	<u>2783</u>
total	86	35	24	27	42049

<sup>1</sup>Total number of pups used in birth rate calculation.

<sup>2</sup>Pups excluded from analysis of reproductive success because; 1) >10lbs at capture (n=16);

<sup>3</sup>because outcome of dependency was not determined (n=18).

<sup>3</sup>pups used in reproductive success analysis.

Table 4. Mean length of reproductive intervals for sea otters at Amchitka Island, Alaska.

Mean length of interval (days) for all dependencies				
Interval	n	$\bar{X}$	rate <sup>1</sup>	SE
Gestation				
non-delayed	37	200		3.7
delayed	3	309		5.4
Dependency	60	126		9.9
Inter-birth	31	341	(1.07)	12.7

Mean length of interval (days) by outcome of dependency									
Interval	n	$\bar{X}$	successful		unsuccessful		unknown		SE
			n	rate <sup>1</sup>	n	rate <sup>1</sup>	n	$\bar{X}$	
Gestation									
non-delayed	12	201	13	5.9	196	7.1	12	203	6.5
delayed	1	299	-	-	--	-	2	314	3.3
Dependency	37	180	23	5.2	40	7.8	-	--	-
Inter-birth	20	383	11	8.1	263	14.8	-	--	-
				(0.95)		(1.39)			

<sup>1</sup>Annual birth rate based on 365 days/mean inter-birth interval.

Table 5. Frequency of radio failures and unresolved disappearances of radio instrumented sea otters by season on Amchitka Island, Alaska. Date of disappearance or failure is based on the date of last radio location. (Winter = October to March, Summer = April to September)

Season	Confirmed failures		Known deaths		Unresolved disappearances							
	%	n	%	n	Total		Females <sup>1</sup>		Males <sup>1</sup>		Weanlings	
					%	n	%	n	%	n	%	n
summer	55	11	25	1	24	6	33	6	10	1	25	2
winter	45	9	75	3	76	19	67	9	90	9	75	6

<sup>1</sup>Includes adults and juveniles >1 year old.

Table 6. Total disappearance rate, confirmed radio failure rate and unresolved disappearance rate of radio instrumented sea otters at Amchitka Island, Alaska from July 1992 to June 1994.

Sex - age	Total radio implants		Total disappearance rate <sup>1</sup>		Confirmed failure rate		Unresolved diss. rate <sup>2</sup>		Known deaths	
	N	miss/N	n	rate <sup>1</sup>	fail/miss	n	unres/N	n	n	n
Females										
Pups	6	0.67	4		0.50	2	0.50	2	0	0
Juveniles	9	0.33	3		1.00	3	--	0	0	0
Adults	<u>34</u>	<u>0.50</u>	<u>17</u>		<u>0.47</u>	<u>8</u>	<u>0.26</u>	<u>9</u>	<u>1</u>	<u>1</u>
Total	49	0.49	24		0.54	13	0.22	11 <sup>3</sup>	1	47
Males										
Pups	5	0.80	4		--	0	0.80	4	1	1
Juveniles	5	0.80	4		0.50	2	0.40	2	1	1
Adults	<u>21</u>	<u>0.62</u>	<u>13</u>		<u>0.38</u>	<u>5</u>	<u>0.38</u>	<u>8</u>	<u>1</u>	<u>1</u>
Total	31	0.68	21		0.33	7	0.45	14 <sup>3</sup>	3	3
Males <sup>4</sup>										
territorial	7	0.57	4		0.50	2	0.29	2	0	0
non-terr.	14	0.64	9		0.33	3	0.43	6	1	1

<sup>1</sup>Excludes known deaths.

<sup>2</sup>Potential mortalities.

<sup>3</sup>Comparison significantly different (Fisher's exact 2-tailed, P = 0.05).

<sup>4</sup>Adults only.

Table 7. Duration of postweaning contact with radio instrumented sea otter pups on Amchitka Island, Alaska.

Capture date	Total <u>implanted</u> N	Duration (days) of <u>postweaning contact</u>		Date of last <u>location</u> median date	Known <u>deaths</u> n
		$\bar{X}$	minimum maximum		
July 1992	6	74	0 142	11/16/92	1
1993	5	218	106 322 <sup>1</sup>	03/30/94	0

<sup>1</sup>Study ended with 2 pups still alive and transmitting in June 1994.

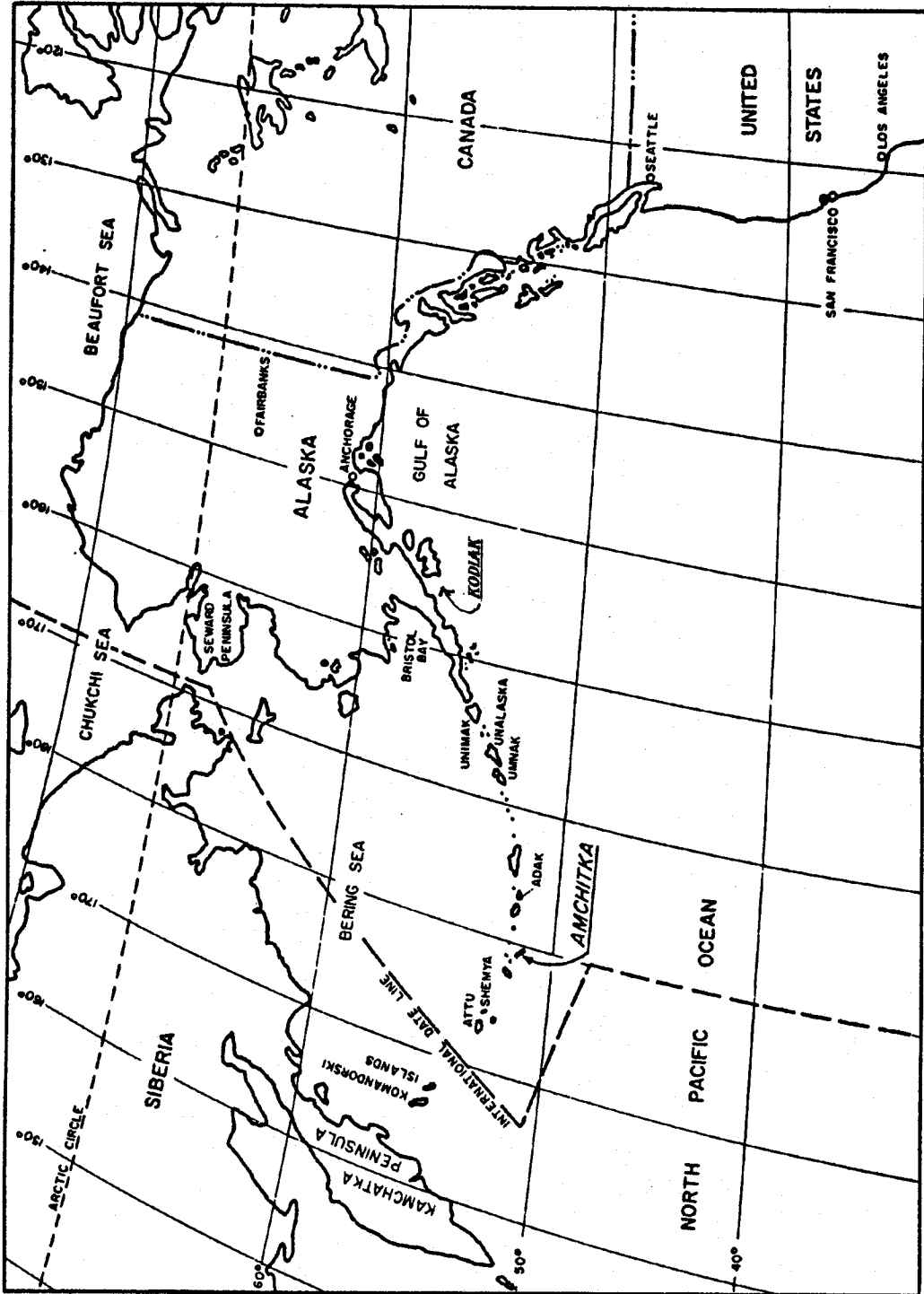


Fig. 1. Study area map of Alaska study sites.

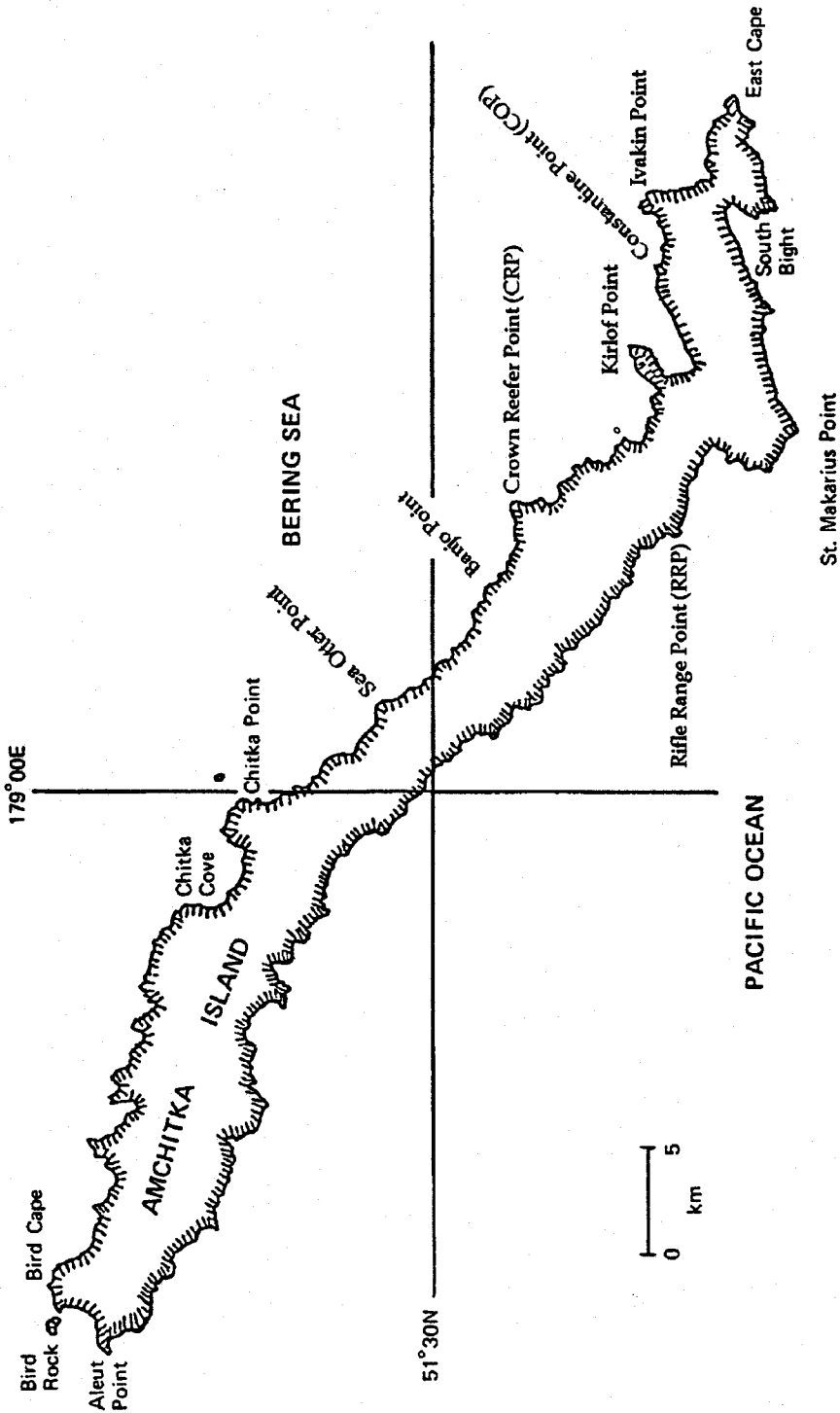
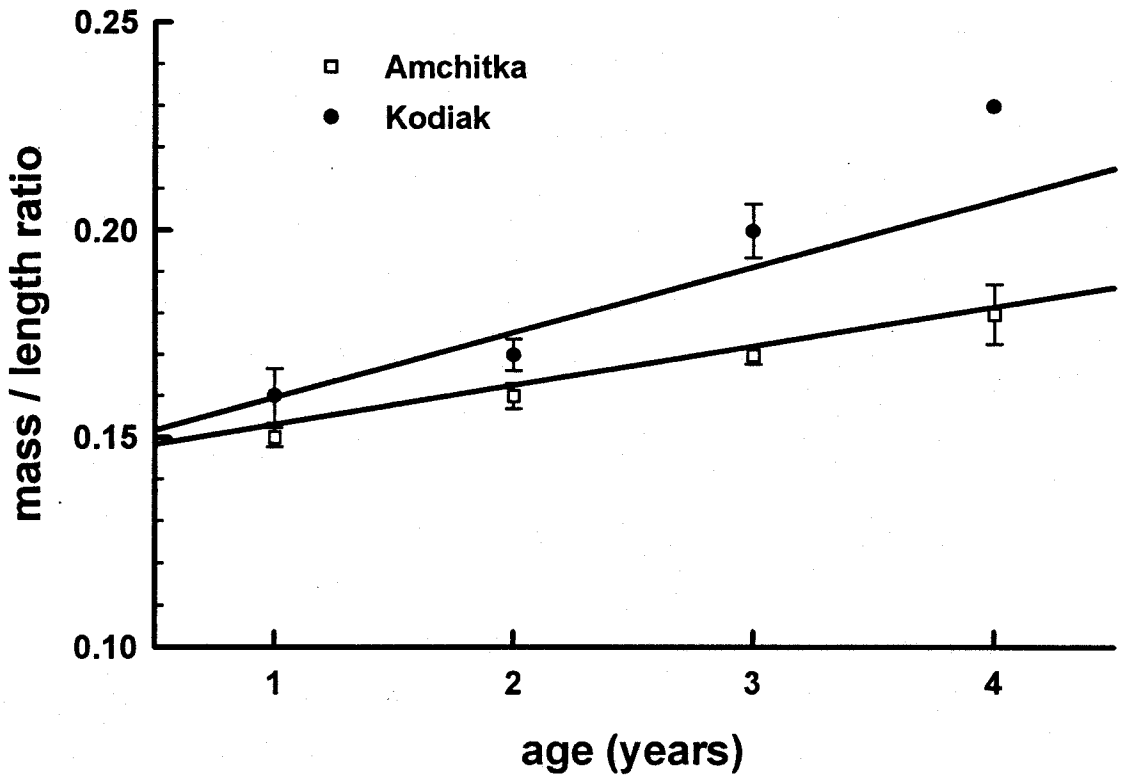


Fig. 2. Study area map for the sea otter telemetry study on Amchitka Island, Alaska.





**Fig. 3.** Mass/length ratios of young, non-pregnant female sea otters at Kodiak Island, Alaska (Monson and DeGange in press), and at Amchitka Island, Alaska. Lines are regressions through all data for each age while points are the mean mass/ratio  $\pm$ SE for each age-class.

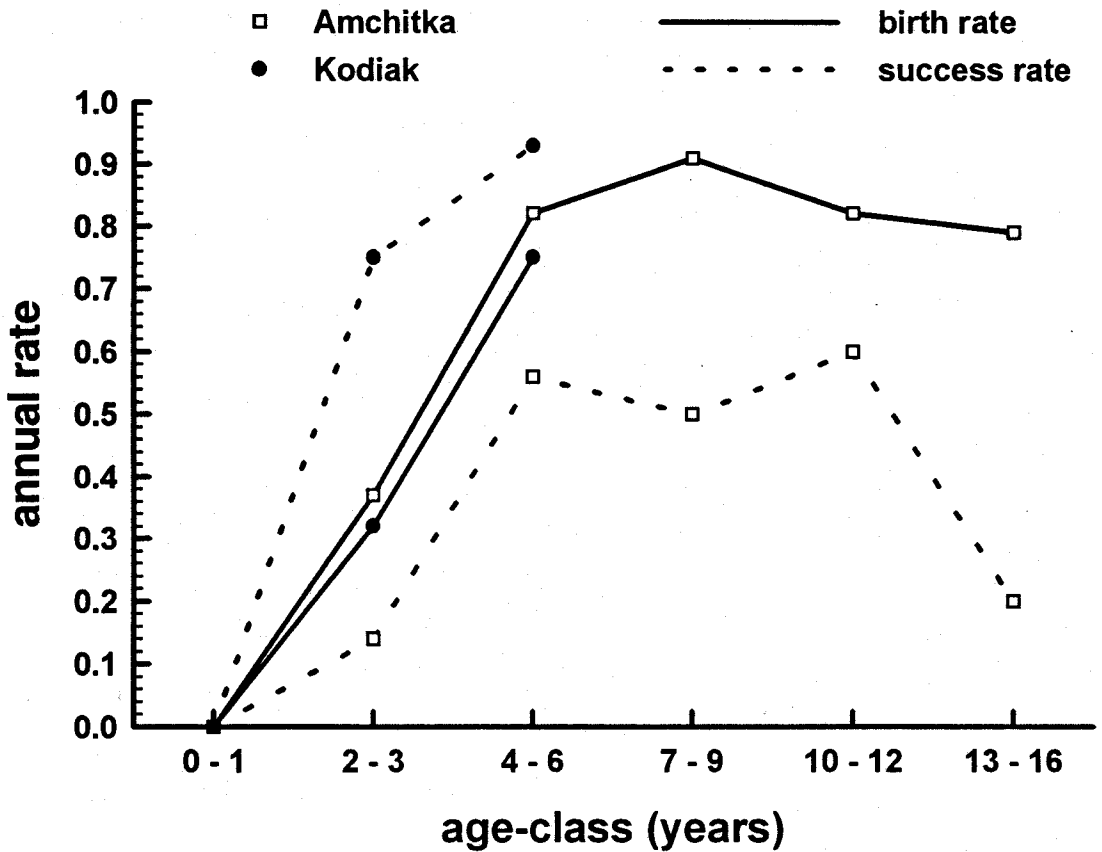
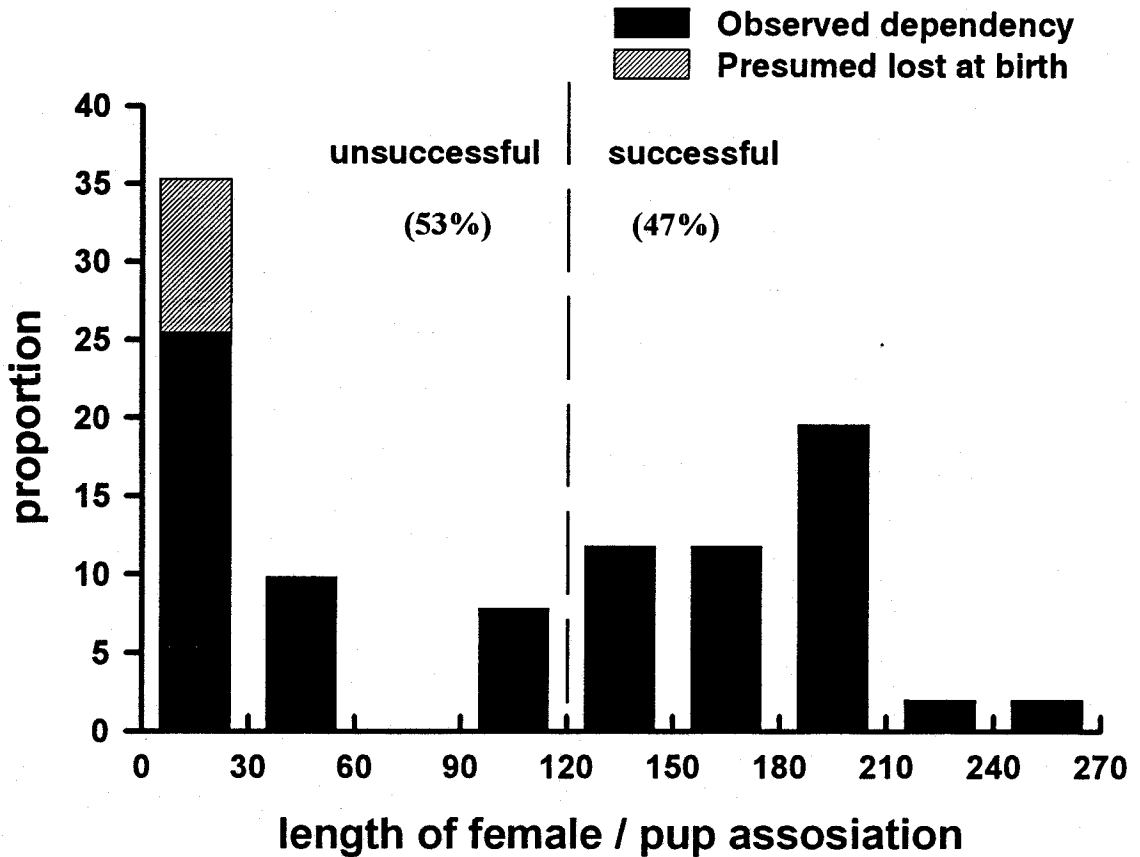
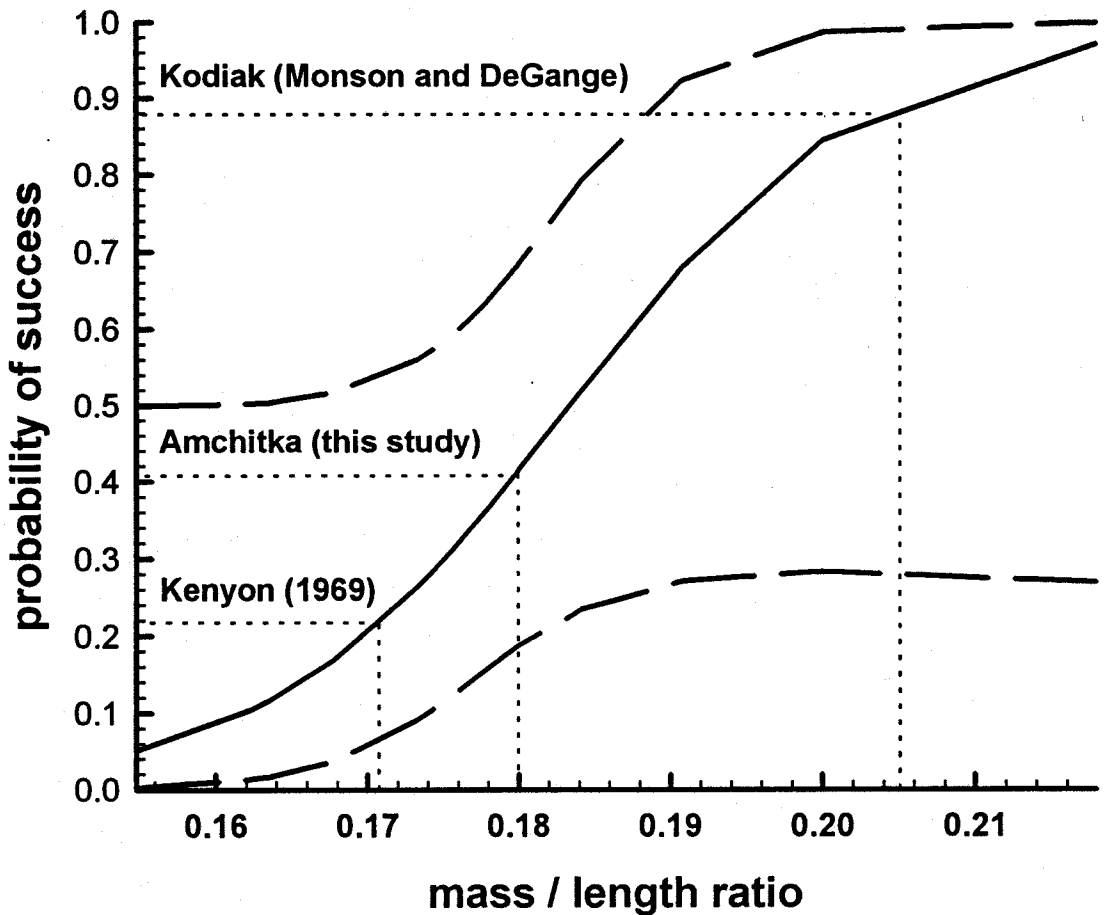


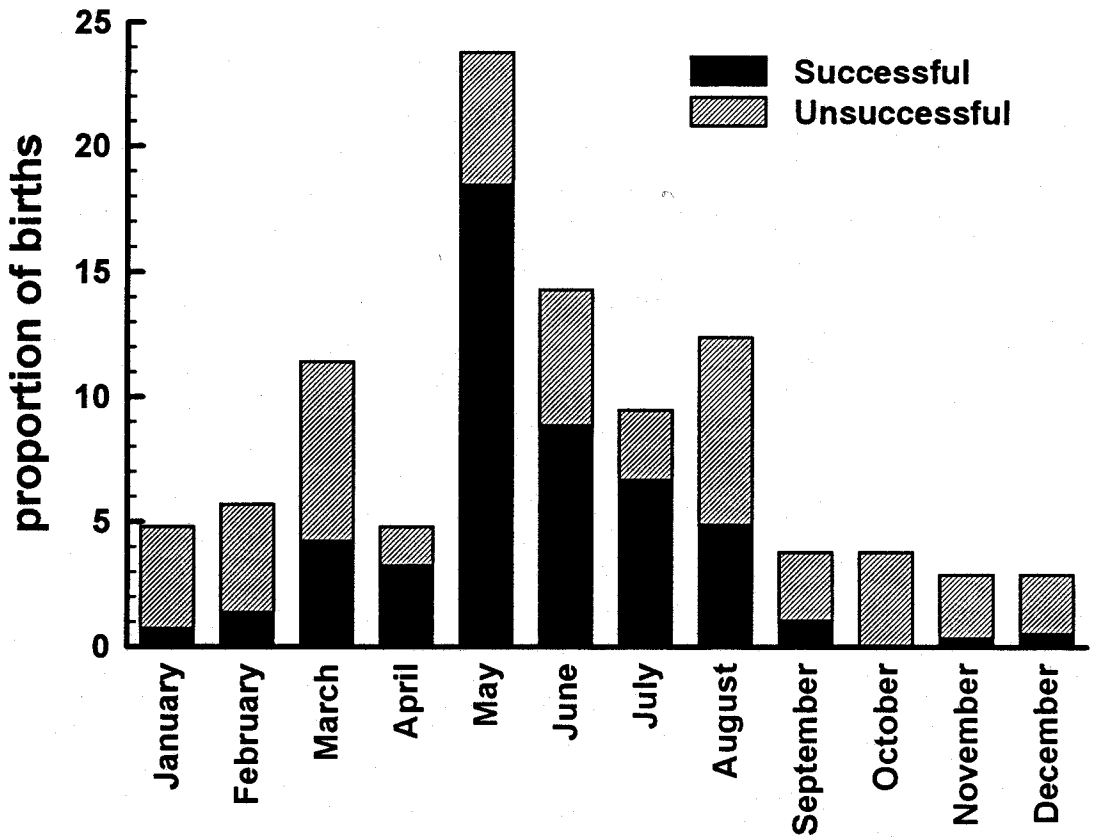
Fig. 4. Annual birth rates and reproductive success rates of female sea otters from Kodiak Island (Monson and DeGange in press), and from Amchitka Island, Alaska. (no female otters > 6 yrs old were captured in Kodiak)



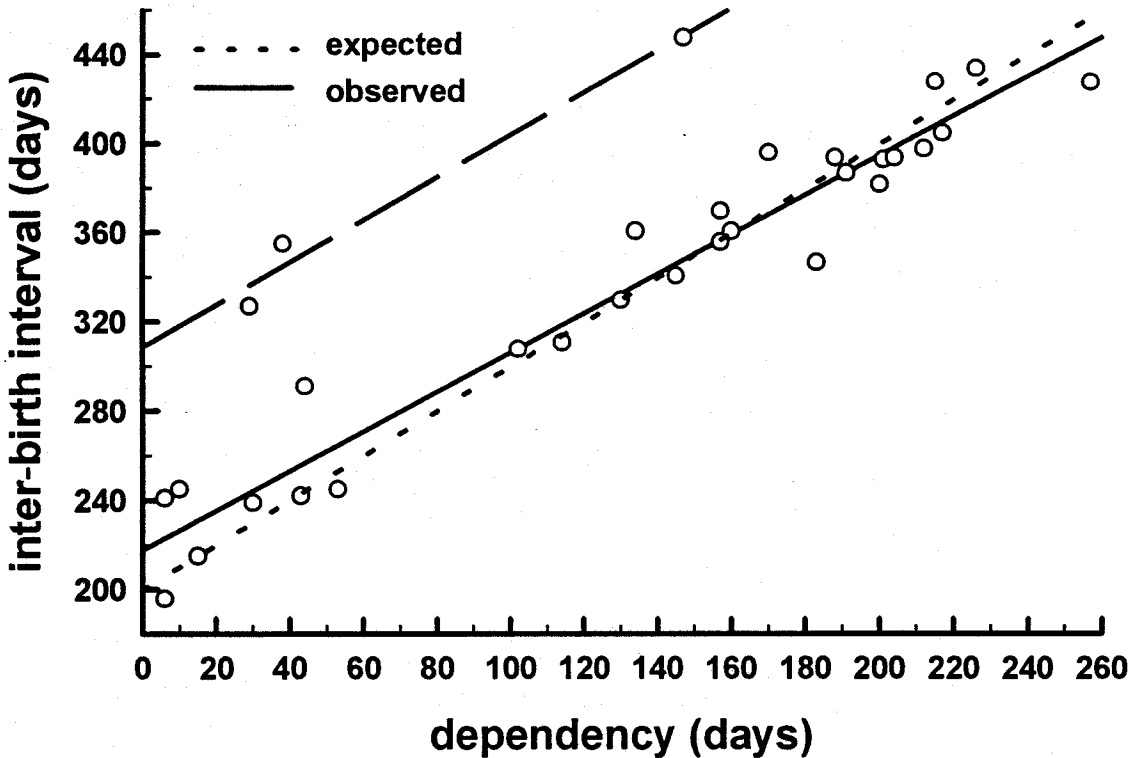
**Fig. 5. Distribution of pup dependency lengths ( $n = 51$ ) for sea otter pups born on Amchitka Island, Alaska from 1992-1994. Minimum age for successful weaning assumed to be 120 days. Excludes pups capture as dependents and >10lbs at capture ( $n = 16$ ), and pups lost within a month of capture ( $n = 3$ ).**



**Fig. 6. Relationship between reproductive success and mass/length ratio for sea otters at Amchitka Island, Alaska (logistic regression;  $P=0.07$ ,  $-2 \log L=18.6$ ,  $\text{Chi SQ}=5.5$  1df,  $P=0.02$ ). Dashed lines indicate 95% CI. Dotted lines are predicted mean success rates for sea otters at Amchitka (this study and from the early 1960's), and at Kodiak Island, Alaska, based on mean mass/length ratios of adult females captured in each population.**



**Fig. 7. Monthly distribution of sea otter pup births at Amchitka Island, Alaska from July 1992 to June 1994. Monthly proportion based on 105 observed or calculated births. Monthly success rates based on 51 births of known outcome.**



**Fig. 8. Relationship between inter-birth interval and length of pup dependency periods for sea otters at Amchitka Island, Alaska. Dotted line ( $y = 200 + x$ ) is the expected relationship if females are always impregnated soon after mother/pup separation. Solid line is the regression through all data except those showing delayed impregnation ( $y = 218 + 0.89x$ ;  $r^2 = 0.94$ ,  $P < 0.001$ ,  $n = 28$ ). The dashed line is the relationship through the data indicating delayed impregnation ( $y = 309 + 0.95x$ ;  $r^2 = 0.95$ ,  $P = 0.098$ ,  $n = 3$ ).**

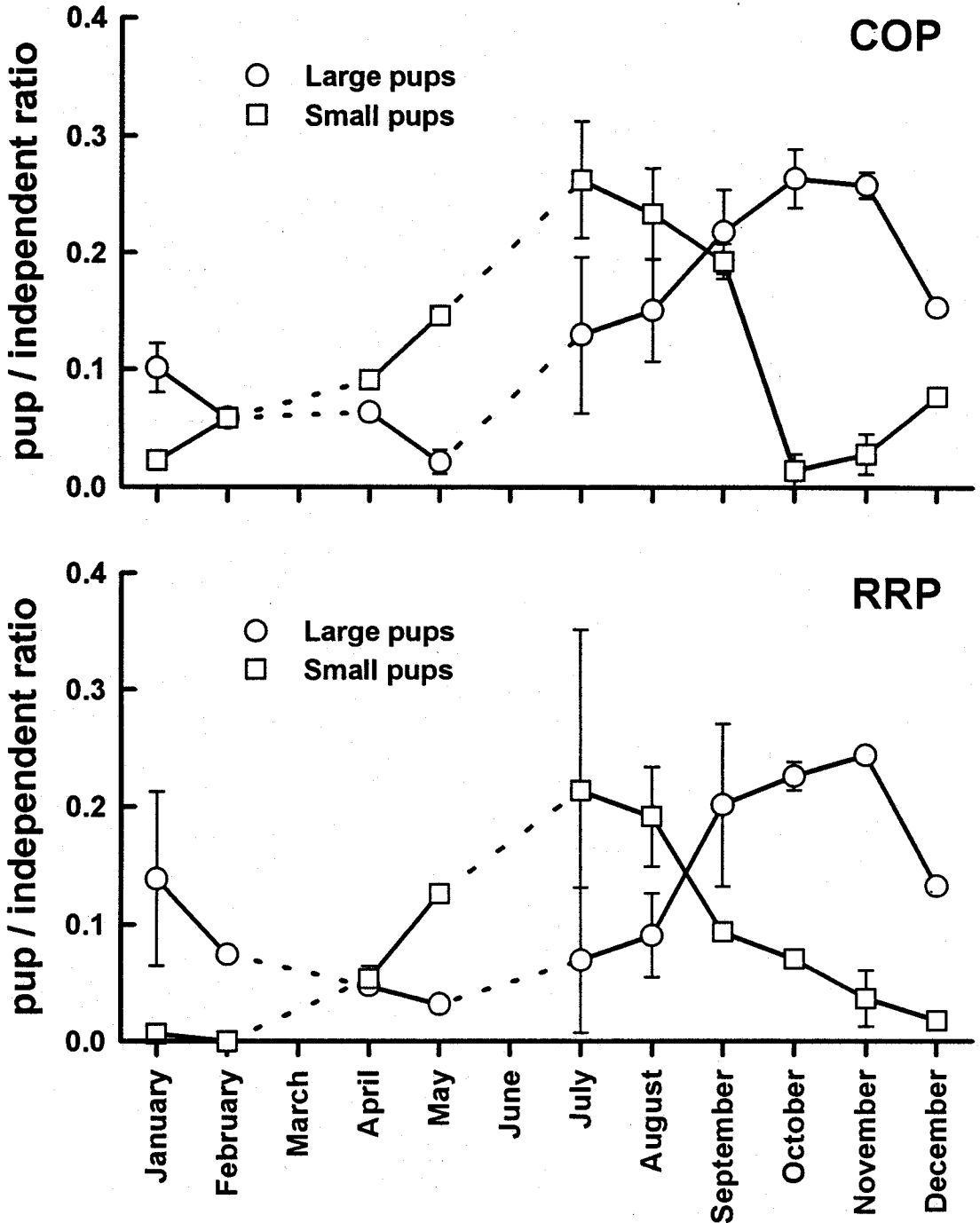
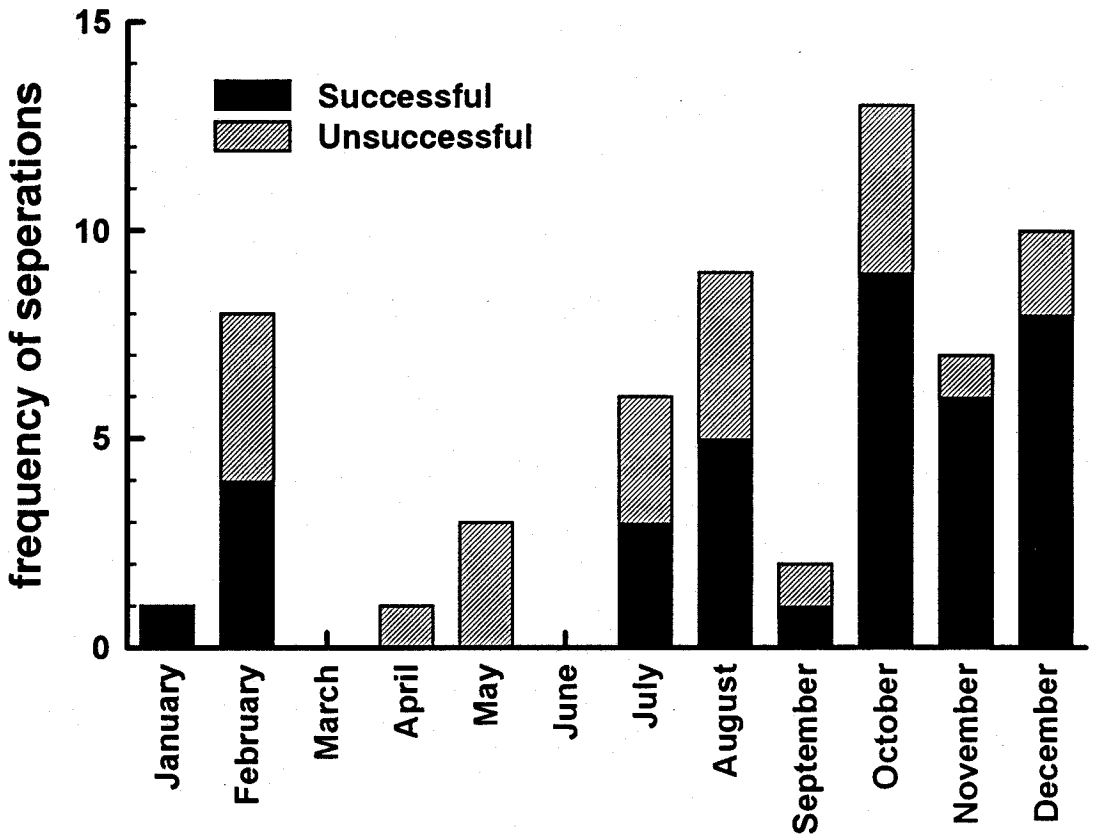
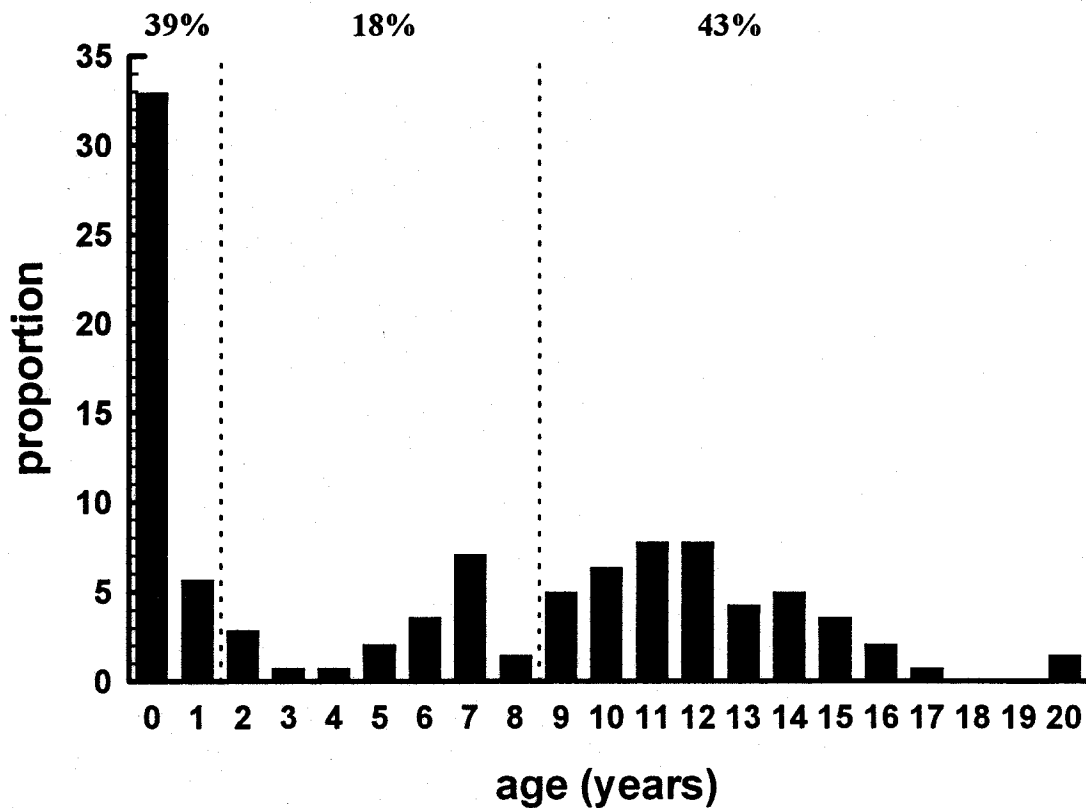


Fig. 9. Monthly ratio of pups/independent adults from sea otter surveys at Constantine Point (COP) and at Rifle Range Point (RRP) on Amchitka Island, Alaska. Points are the mean ratio  $\pm$ SE. Dashed lines indicate a break in surveys.



**Fig. 10. Monthly distribution of mother/pup separations estimated from radio tagged female sea otters at Amchitka Island, Alaska. The distribution is the number of successful and unsuccessful dependencies ending during each month (n = 60).**





**Fig. 11. Age distribution of sea otters found dead on Amchitka from 1992 to 1994 (n = 143). Percentage between vertical lines indicate relative numbers of young, prime and old age-class animals in the distribution.**

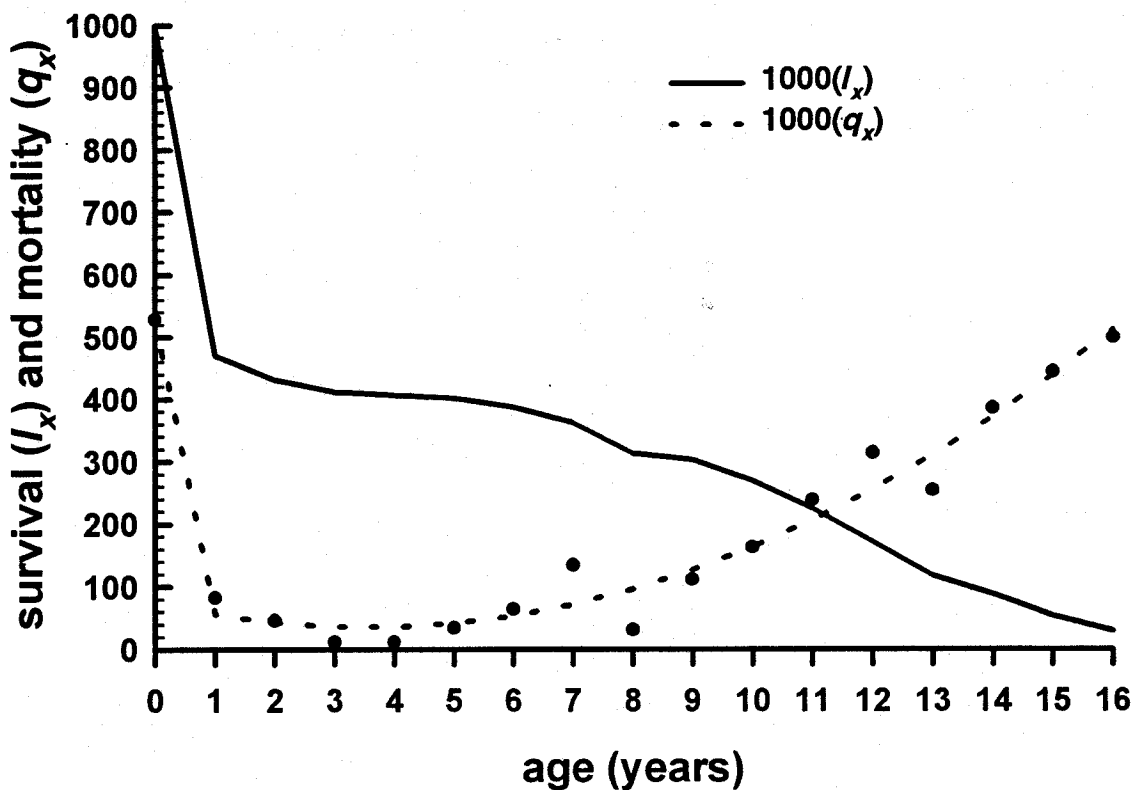


Fig. 12. Survival functions for sea otters living at Amchitka Island, Alaska. Curves based on age distribution of sea otters found dead with survival to age 1 adjusted by the estimated reproductive success rate of radio instrumented females.  $q_x$  curve smoothed with least squares to  $q_x$  values for each age-class (points).