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Life history plasticity and population regulation in sea otters

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We contrasted body condition, and age-specific reproduction and mortality between a growing population of sea otters (*Enhydra lutris*) at Kodiak Island and a high-density near-equilibrium population at Amchitka Island, Alaska. We obtained data from marked individuals, population surveys, and collections of beach-cast carcasses. Mass:length ratios indicated that females (but not males) captured in 1992 at Amchitka were in poorer condition than those captured at Kodiak in 1986–1987. In 1993, the condition of females at Amchitka improved in apparent response to two factors: (1) an episodic influx of Pacific smooth lumpsuckers, *Aptocyclus ventricocus*, from the epi-pelagic zone, which otters consumed; and (2) an increase in the otters' benthic invertebrate prey resulting from declining otter numbers. Reproductive rates varied with age (0.37 [CI = 0.21 to 0.53] births female^{-1} yr^{-1} for 2–3-yr-olds, and 0.83 [CI = 0.69 to 0.90] for females ≥ 4 yr old), and were similar at both areas. Weaning success (pups surviving to ≥ 120 d), in contrast, was almost 50% lower at Amchitka than at Kodiak and for females ≥ 4 yr of age was 0.52 (CI = 0.38 to 0.66) vs 0.94 (CI = 0.75 to 0.99), respectively. Sixty-two percent of the preweaning pup losses at Amchitka occurred within a month of parturition and 79% within two months. Postweaning survival was also low at Amchitka as only 18% of instrumented pups were known to be alive one year after mother-pup separation. Adult survival rates appeared similar at Amchitka and Kodiak. Factors affecting survival early in life thus are a primary demographic mechanism of population regulation in sea otters. By maintaining uniformly high reproductive rates over time and limiting investment in any particular reproductive event, sea otters can take advantage of unpredictable environmental changes favorable to pup survival. This strategy is consistent with predictions of "bet-hedging" life history models.

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Resource availability (e.g., food, space or some other limiting resource) affects the life history parameters of most, if not all animals (see Riedman 1981, Clutton-Brock 1988, and Boutin 1990 for reviews). The nature of such life history variation is a reflection of two counteracting historical processes: the conservative influence of an organism's evolutionary history and the diversifying influence of environmental change (Levins 1968, Negus and Berger 1987, Bronson 1989, Stearns 1989, 1992). Broadly viewed, life history variation results in changes in age-specific probabilities of reproduction and mortality. Food availability affects the balance of energy available for reproduction vs growth and maintenance (i.e. survival; Clutton-Brock et al. 1983), and thus can have a strong influence on life history parameters. The effects of variable food resources on individual life history parameters have commonly been studied in rodents (Dobson and Kjelgaard 1985, Wauters and Dhondt 1989) and ungulates (Albon et al. 1983, Skogland 1985, Clutton-Brock 1988). Less

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is known about life history variation in the carnivores because of their scarcity and secluded lifestyles, but several species have shown demographic responses to variation in food availability (Harrington et al. 1983, Todd and Keith 1983, Elowe and Dodge 1989, Lindström 1989, Angerbjörn et al. 1991). One approach to documenting the effects of food availability is to contrast life history and demographic parameters between growing populations (non-food-limited) and equilibrium populations (food-limited). Such contrasts are valuable because they: 1) illustrate the demographic mechanisms of population regulation; 2) define relevant life history criteria for assessing population status; and 3) provide some indication of the extent to which variation in food limitation has acted to shape life history.

The history of sea otters in the North Pacific Ocean provides an unusual opportunity for contrasting life history strategies in relation to population status (i.e., food availability). Sea otters were hunted to near extinction in the maritime fur trade (Kenyon 1969). Following protection in 1911, the scattered remnant populations began to grow. Several contemporary populations recovered to pre-exploitation (equilibrium) levels and for these food is an important limiting resource (Kenyon 1969, Garshelis et al. 1984, Estes 1990, Bodkin et al. 2000). Other populations are below equilibrium density and increasing (Rotterman and Simon-Jackson 1988, Estes 1990). This spatio/temporal pattern of overexploitation and recovery has been used as a natural experiment to evaluate the role of sea otter predation in structuring nearshore communities over multiple trophic levels (Estes and Palmisano 1974, Duggins 1980, Breen et al. 1982, Duggins et al. 1989, Kvitek et al. 1992, Estes and Duggins 1995). Here we use the same approach to evaluate how demographic changes act to limit the growth of populations as they approach equilibrium. Specifically, we contrast age-specific birth rate, survival, and reproductive success between the near-equilibrium density population at Amchitka Island and the expanding population at Kodiak Island, Alaska (Monson and DeGange 1995).

We may view life history responses to environmental conditions as facultative (i.e., adjustments under the "control" of the organism) or obligatory (constraints forced on the organism by the environment). Distinguishing between these two mechanisms can be problematic and the answer depends on the perspective from which one views the question. One approach is to contrast "available" strategies (i.e., those expressed in closely related species) with the strategy actually expressed by the species of interest. This approach may be particularly illuminating where the available strategies or the environmental conditions in which the phylogenetic line occurs are diverse. The otters (*Carnivora*, *Lutrinae*) are well-suited for such an analysis as they occupy a wide range of habitats and use a variety of reproductive strategies. Compared with other mustelids, sea otters are long-lived, mature late in life, and have a long reproductive cycle that often includes an extended period of delayed implantation. Litter size is always one, and survival is generally higher in adults than juveniles. These characteristics are of further interest to life history theory (Stearns 1976) because sea otters represent a transitional form in the evolution of marine living by mammals (Estes 1989, Williams 1999). We discuss our findings in this context by contrasting sea otters with other mustelids (with whom they share a recent common ancestry) on the one hand and with the pinnipeds (with whom the otters share a common environment) on the other.

Materials and methods

Selection acts at the individual level on life history parameters (e.g., reproductive intervals, litter size, timing of births, etc.) which collectively determine population demographics (age-specific birth and death rates). This paper is based on the comparison of both individual life history characteristics and demographic patterns in sea otters between Amchitka and Kodiak islands, Alaska (Fig. 1). The population at Amchitka Island grew rapidly following cessation of hunting in the Pacific maritime fur trade and reached a point of

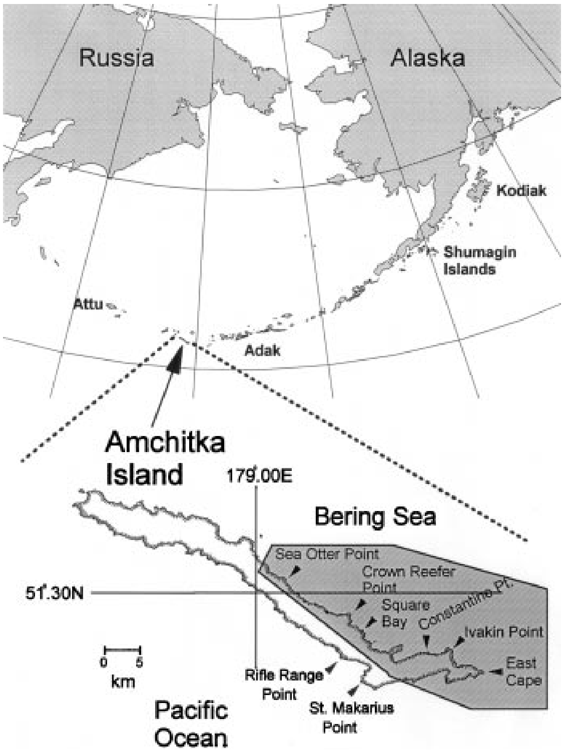

Fig. 1. Map of the study areas in Alaska showing core study sites and place names at Amchitka Island.

food-limitation by the early 1940s (Kenyon 1969), where it remained through the 1980s (Estes 1990). We began field work at Amchitka Island in 1992, assuming that sea otters were at equilibrium density, although data now available suggest that the population at that time was in the early stage of decline (Estes et al. 1998). While the cause of this decline is not certain, evidence suggests increased killer whale predation. In contrast, the Kodiak study, conducted 1986–1989, was done near the front of an expanding sea otter population in the process of reoccupying otter-free habitat. Food was plentiful (Kvitek et al. 1992, Doroff and DeGange 1994) and unoccupied habitat existed within the study area. Monson and DeGange (1995) report the study sites, methods, and the life history and demographic data from Kodiak.

Study area

Amchitka Island is in the Rat Island group of the western Aleutian archipelago (Merritt and Fuller 1977). Most field work was done between Sea Otter Pt. and East Cape along Amchitka's northeast coast (Fig. 1). Sea otters segregate by sex (Kenyon 1969). Male aggregations occurred at Crown Reefer Pt. and East Cape while the remaining areas supported females and territorial males.

Field methods

We captured sea otters at Amchitka in July 1992 and in August 1993 using un-weighted tangle nets and diver-operated traps (Ames et al. 1983). Adults and pups > 9 kg were anesthetized using a combination of fentanyl citrate (RBI, Natick, ME) and diazepam (Steris Laboratories, Inc., Phoenix, AZ), and surgically implanted with radio transmitters (Advanced Telemetry Systems, Inc., Isanti, MN) using procedures described by Williams et al. (1981). To permit visual identification, we marked each instrumented animal with colored flipper tags (Temple Tags, Temple, TX). We marked palpably pregnant females with flipper tags only. Pups < 9 kg were not marked. For each independent otter, we extracted a premolar, and recorded mass and length measurements. Age was estimated from decalcified longitudinal sections of the premolar (Bodkin et al. 1997).

We located radio-instrumented otters using programmable scanning receivers (Advanced Telemetry Systems, Isanti, MN) and marked animals were identified and observed using binoculars and high resolution spotting scopes (Questar Corp., New Hope, PA). Searches were done from the coast by scanning at high points with a handheld yagi antenna, or from a skiff using a twin side-looking antenna array. We attempted telemetric relocations and visual observations of each marked animal at least weekly from July 1992 through March 1994, and once in June 1994. Skiff and road-accessible locations outside the core study area were checked periodically for missing animals. At each relocation, we recorded date, UTM coordinate, presence or absence of a dependent pup, and evidence of mating activity (i.e., the presence of a male consort or a fresh nose injury [Foott 1971]).

We conducted monthly surveys to determine population growth rate and pup:independent ratios in three index areas: 1) between Constantine and Ivakin points; 2) between Rifle Range and St. Makarius points on the south side of the island; and 3) between Square bay and Crown Reefer point (Fig. 1). Beach surveys to recover sea otter carcasses were done monthly in these same areas. We obtained additional carcasses opportunistically or during island-wide searches each spring. The age and sex were determined for each carcass when possible.

Data analysis

We compared mass:length ratios (M/L) of otters at Amchitka with those obtained from Kodiak Island in 1986–1987. Only non-pregnant, non-lactating females were used in this analysis to eliminate the confounding effects of pregnancy status. We used t-tests and general linear models (proc GLM, SAS statistical software) on arcsine-transformed M/L ratios.

We calculated age-specific birth rates as the number of observed births $\text{female}^{-1}\ \text{yr}^{-1}$ (Siniff and Ralls 1991). We inferred a few births from behavioral clues of the female although no pup was observed. That is, if we observed a female copulating, in the presence of male consorts, or with fresh nose wounds at a time consistent with the expected parturition date for a particular female we assumed she had a pup which died at or soon after parturition, and thus had come into estrus. We may still have missed pregnancies that terminated prematurely, but we have no way to measure premature loss rates. Logistic analysis and the Wald Chi-Square statistic were used to compare populations and determine birth rate confidence intervals. We never observed parturition so exact birth dates were unknown. However, maximum and minimum intervals could be determined from resight records and we estimated inter-birth intervals as the midpoints between these. We divided the inter-birth interval into two non-overlapping periods: impregnation to birth (gestation) and birth to separation (dependency). We provide means and standard errors for estimates of reproductive intervals but do not conduct statistical analysis due to the potential for imprecision of interval estimates.

We estimated pup survival from birth to weaning as the ratio of pups surviving ≥ 120 d to total pups born. That is, we assumed pups who remained with their

Table 1. Summary of tagging information for sea otters captured at Amchitka Island, Alaska in 1992 and 1993.

Year	Age class	Total captured	Radio tagged	Flipper tagged only	Not marked
1992	Adult female	43	33	10	–
	Adult male	21	21	–	–
	Juvenile female	8	8	–	–
	Juvenile male	5	5	–	–
	Female pup	9	2	–	7
	Male pup	8	4	–	4
1993	Adult female (2 recaptures)*	14	2	11	–
	Adult male (1 recapture)*	1	0	–	–
	Juvenile female	1	0	1	–
	Female pup	3	3	–	–
	Male pup	2	2	–	–
Total		115	80	22	11

* One recaptured female had only been flipper tagged in 1992 and was given a radio in 1993 while a second female and a male already had tags and a radio from the previous year.

mothers < 120 d died whereas pups surviving ≥ 120 d were successfully weaned (Riedman et al. 1994). Pups remaining with their mothers ≥ 120 d have been known to survive into adulthood while this is not the case for pups with shorter dependencies. For the purposes of determining preweaning survival rates we excluded births that occurred during the last 120 d of our study where outcomes of dependency were unknown. We also excluded pups weighing > 4.5 kg (approximately 30 d old) at capture because the probability of weaning success increases beyond this age (Siniff and Ralls 1991, Riedman et al. 1994). These pups had already passed the critical survival period before inclusion in the study, and thus leaving them in the analysis would bias preweaning survival estimates. We used logistic analysis and the Wald Chi-Square statistic to compare preweaning survival rates and estimate confidence intervals around these survival estimates. Fisher's exact tests (Sokal and Rohlf 1995) were used to evaluate differences in proportions of pups surviving by season (April–September – summer; and October–March – winter), between years (1992–1993 vs 1993–1994) at Amchitka, and between Kodiak and Amchitka. We estimated birth dates of pups captured as dependents from their mass at capture and growth rates reported by Monnett et al. (1991). We used logistic regression to examine the effect of female M/L ratio (measured at capture) on subsequent pup survival.

Radios had an expected transmission life of two years. However, a high rate of known, premature radio failures compromised the survival analysis from the tagged population at Amchitka. Thus we used the age-at-death distribution (based on tooth analysis) of sea otters found dead on Amchitka beaches to estimate the number surviving at age x (l_x), the number dying between age x and $x+1$ (d_x) and the age-specific mortality rate (q_x; Caughley 1966, 1977). Zero-age otters are probably under-represented in carcass collections because of their small size and the increased likelihood of removal by scavengers, thus biasing estimates of l_x and d_x for all other age classes. We conservatively adjusted the number of zero-age carcasses upward such that q_0 was equal to the preweaning mortality rate. From this adjusted age distribution, the age-specific survival rate was estimated using eq. (9) from Udevitz and Ballachey (1998);

$$\hat{s}_x = 1 - \frac{y_{xt}\lambda^x}{\sum_{k=x}^{w} y_{kt}\lambda^k}, \quad x = 0, \ldots, w-1. \tag{1}$$

where $\hat{s}_x$ the age-specific survival rate when y is the number of carcasses in age-class x at time t with a population growth rate of λ.

This calculation allowed us to account for a general population decline of approximately 8% per year from 1992 to 1997 (GLM, $P = 0.01$, $R^2 = 0.37$) as determined from counts in local index areas. This analysis assumes a stable age structure which may not be true for this population, and sea otters in general, due to variations in juvenile survival. However, if we assume juvenile survival varies around some mean, then over time we may expect the age structure to vary around a "stationary distribution" (Caswell 1989: 208–212). Therefore we analyzed age-at-death distributions separately for each year of carcass collections (1992–1994), and calculated the mean age-specific survival rate. Mean values were smoothed and the confidence interval estimated using non-linear least squares (proc NLIN, SAS statistical software). We present q_x values as they are the best indicators of age-specific mortality patterns, and not subject to biases associated with the zero age-class (Caughley 1966).

Results

Mass:length analysis

At Amchitka we captured 94 sea otters in July 1992 and 21 (including three recaptures) in August 1993 (Table 1). Thirty-five adult females, eight juvenile females, and 11 dependent pups were instrumented. We marked 22 additional females with flipper tags only, and 11 dependent pups < 9 kg were not marked at all due to their small size at capture. Twenty-six adult and juvenile males were also tagged and instrumented. Descriptions of marked animals at Kodiak are provided in Monson and DeGange (1995). We captured no females > 4 yr old at Kodiak as the capture effort there focused on areas inhabited primarily by young animals (i.e., newly occupied habitat).

Mass:length ratios were similar for 1-yr-olds at Amchitka and Kodiak. However, the rate of M/L gain with age was significantly less for females captured at Amchitka in 1992 than for females captured at Kodiak (Fig. 2, GLM, $F_{\text{age} \times \text{location}} = 6.89$, df = 1,41, $P = 0.01$), and by three years of age females at Kodiak had significantly higher M/L ratios than same age females at Amchitka (Fig. 2, $F_{\text{age 3}} = 13.5$, df = 1,10, $P = 0.004$). Using 3- and 4-yr-olds as a conservative indicator, non-pregnant adult females at Kodiak were longer (128 vs 124 cm, $t_{31} = 2.36$, $P = 0.025$) and heavier (26.2 vs 22.3 kg, $t_{31} = 4.47$, $P < 0.001$) and had significantly higher M/L ratios (0.205 vs 0.180 kg/cm, $t_{31} = 4.12$, $P < 0.001$) than non-pregnant adult females at Amchitka. The mean M/L of non-pregnant, adult females captured at Amchitka increased significantly from 1992 to 1993 ($\bar{X} = 0.180$ to 0.204 kg/cm, $t_{33} = 4.03$, $P < 0.001$), and in 1993 was nearly identical to that measured at Kodiak. Furthermore, two adult females, measured initially in 1992 and recaptured in 1993, had gained 1.8 and 2.3 kg, thus increasing their M/L ratios by 0.02 kg/cm. The increased M/L ratios observed in the second year of study at Amchitka suggests the differences between the populations were not simply due to genetic variation.

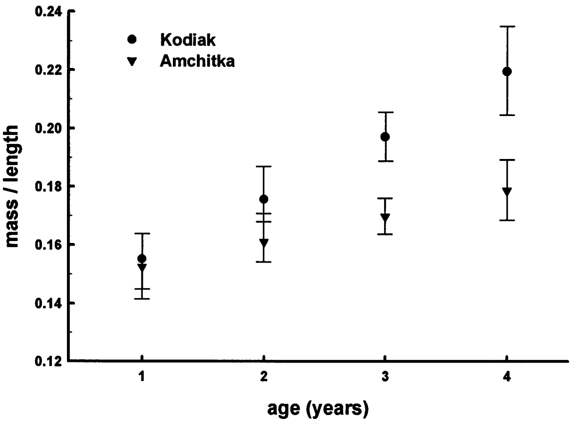

Fig. 2. General linear model of M/L ratios of young, non-pregnant female sea otters at Amchitka and Kodiak islands, Alaska. Values are predicted outcome of the model with associated confidence intervals for each age class. The slopes of the two regressions are statistically different (GLM, $F_{\text{location} \times \text{age}} = 6.89$, 1 df, $P = 0.01$).

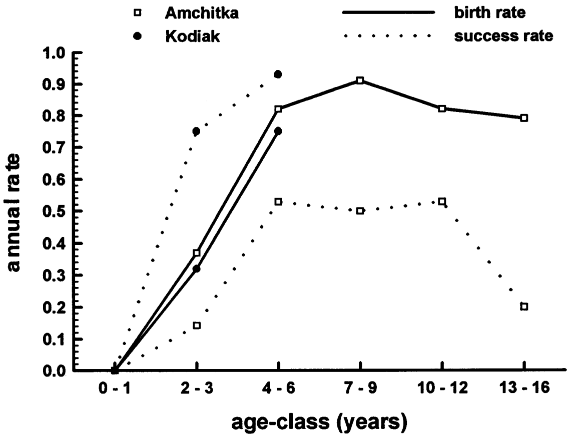

Fig. 3. Annual birth rates and weaning success rates of female sea otters at Amchitka and Kodiak islands, Alaska. Data from Kodiak Island are from Monson and DeGange (1995). No female otters > 4 yr old were captured at Kodiak Island. Confidence intervals were omitted for clarity.

Reproduction

Birth rates and reproductive success

Fifty marked females were observed with 81 pups (including 22 pups captured as dependents) during the study at Amchitka. We assumed another five pups were born and lost based on their mothers' behaviors. Birth rates (births female^{-1} yr^{-1}) at Amchitka increased with age from 0.37 (CI = 0.21 to 0.53) for 2- and 3-yr-olds to 0.83 (CI = 0.69 to 0.90) for $\geq$ 4-yr-olds, and these age-specific birth rates were nearly identical with those at Kodiak (Fig. 3, logistic regression, $P = 0.54$). Similarly, reproductive intervals for sea otters at Kodiak and Amchitka did not appear to differ. The length of gestation averaged 201 ± 6 d at Amchitka vs 218 ± 14 d at Kodiak, though the length of dependency for successfully weaned pups tended to be shorter at Kodiak (153 ± 12 d) than at Amchitka (180 ± 5 d). Imprecision in these estimates may account for the differences (particularly for gestation) rather than inherent biological differences. Inter-birth intervals for successful pregnancies at Amchitka and Kodiak were 383 ± 8 d and 370 ± 9 d, respectively. At Amchitka, females that lost their pups soon after parturition usually came into estrous immediately afterwards and had a mean inter-birth interval of 263 ± 15 d.

In contrast to other reproductive parameters, at least 83% (19 of 23) of the pups born to marked females at Kodiak survived to weaning, whereas only 47% (24 of 51) of the pups born at Amchitka survived to weaning age. Most preweaning pup losses occurred within two months of parturition (Table 2). Age-specific weaning success was lower at Amchitka than at Kodiak (logistic regression, $P = 0.003$), but similar to Kodiak increased with age (Fig. 3). Weaning success ranged from 0.14 (CI = 0.02 to 0.58) for 2- to 3-yr-olds to 0.56 (CI = 0.41

Table 2. Frequency distribution of 61 pup dependencies (in d) for pups born to marked sea otters at Amchitka Island from 1992 to 1994.

Length	0–30	31–60	61–90	91–120	121–150	151–180	181–210	211–240	241–270
Number	18[1]	5	0	6	7	9	16	5	1

[1] Includes five pups never observed but assumed lost immediately following birth.

to 0.71) for 4- to 12-yr-old females, then appeared to declined for females >12 yr (0.20, CI = 0.03 to 0.69). Weaning success in year t was not correlated with success in year $t-1$, but was related to M/L ratios of the females at the time of capture (Fig. 4; logistic regression, $P=0.07$). The survival rate of summer-born pups at Amchitka (0.65, $n=31$) was significantly greater than that of winter-born pups (0.20, $n=20$; Fisher's exact test, $P<0.004$). Pups born between October and January at Amchitka had the lowest probability of survival (0.11, $n=9$).

Because females at Amchitka had significantly higher M/L ratios in 1993 than in 1992, we examined weaning success between years. Only the summer and fall data were comparable as no information was available for winter or spring 1992. Birth rates for 1992 and 1993 were similar (0.80 vs 0.85, respectively) whereas weaning success was 0.29 and 0.54, respectively. Although these figures suggest that pup survival was greater in 1993 than 1992, the small sample sizes resulted in a test of low power (Fisher's exact test, $P=0.38$; $1-\beta=0.18$ at $\alpha=0.05$).

Gestation and reproductive synchrony

Mean period of gestation at Amchitka was 200 ± 4 d and showed no relationship to female age, length of previous pups' dependency (Fig. 5) or month of conception. Gestation did tend to decrease with increased M/L but not significantly so (GLM, $F=2.55$, df = 1, $P=0.15$). This analysis excluded three females that had extended inter-birth intervals (~ 300 d) and six adults not observed with pups for extended periods (>250 d). Two of these were captured as adults yet not observed with a pup throughout the study period. These individuals tended to have lower M/L ratios than females with "normal" reproductive intervals (0.171 vs 0.186 kg/cm, $t_{22}=1.71$, $P=0.1$).

Pups were born to tagged females throughout the year but monthly birth rates were highest in May, a pattern confirmed by pup:independent ratios in monthly surveys (Table 3). The seasonal distribution of births was significantly different from uniform (G-test, $P<0.001$), and led to a similar peak in mother/pup separations centered in October (Table 3).

Postweaning and adult survival

No dependent pups instrumented in summer 1992 ($n=6$) were known to be alive by June 1993, but two of five pups instrumented in summer 1993 were still alive in June 1994. We did not find missing pups during island-wide searches so dispersal was not a likely explanation for weanling disappearances. However, the recovery of the carcass confirmed only one radio-tagged weanling death. We recovered the carcasses of only two radio-tagged adults. However, three of four known mortalities and 76% of radio disappearances occurred during winter when we may expect most mortality to occur (Kenyon 1969).

Thirteen of 156 beach-cast carcasses were relatively fresh, but causes of death could not be determined for any of these. Most remains (89%) were weathered bones and often included the skull only (76%). Thus, the survival function obtained from these specimens was indicative of a time prior to our field work. We do not know how long a skull persists on these beaches, but few beaches are protected from heavy wave action during winter storms and we assume most disarticulated bones are destroyed or removed each year. The overall age distribution of the recovered carcasses comprised 39% young (<2 yr), 18% prime (2–8 yr), and 43% old (>8 yr) age-class animals (Fig. 6). The q_x function for sea otters at Amchitka indicates that mortality was high during the first year of life, declined abruptly after that and was approximately 5% yr^{-1} to

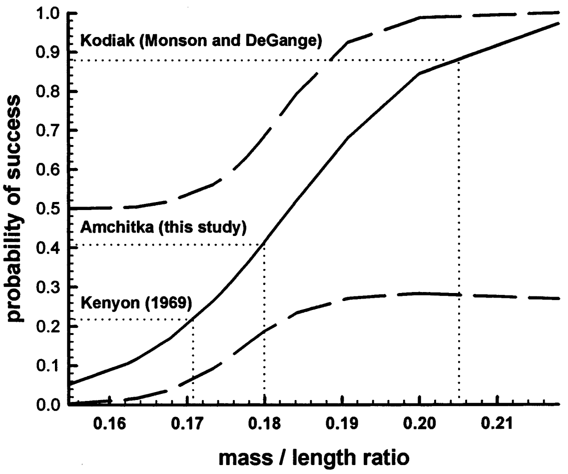

Fig. 4. Relationship (logistic regression) between weaning success and female M/L ratio for sea otters at Amchitka Island, Alaska. Dashed lines are 95% confidence intervals. Dotted lines are predicted success rates for sea otters at Amchitka (this study and for Kenyon's [1969] data from the early 1960s), and at Kodiak islands, based on mean M/L ratios of adult females captured in each population.

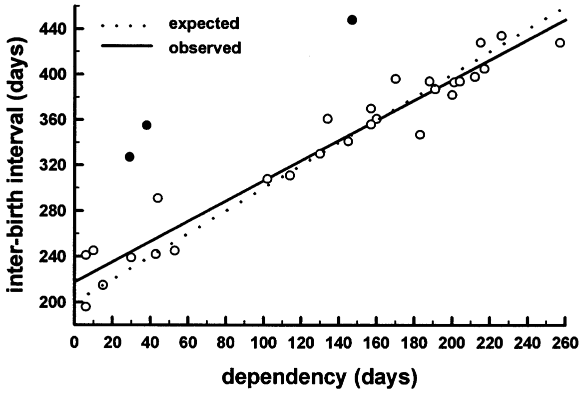

Fig. 5. Relationship between inter-birth interval and length of pup dependency for sea otters at Amchitka Island, Alaska. Dashed line indicates expected relationship if females are always impregnated immediately after female/pup separation. Solid line is regression through all data except those showing delayed or extended gestation (solid dots).

age four, after which it slowly increased to approximately 20% yr^{-1} by age ten and increased more rapidly after age 11 (Fig. 7).

Discussion

Life history plasticity

Our assessment of life history plasticity in the sea otter is based on two comparisons, one planned and the other fortuitous. The planned comparison was between the near-equilibrium population at Amchitka (Kenyon 1969, Estes 1990) and the growing population at Kodiak (Kvitek et al. 1992, Doroff and DeGange 1994, Monson and DeGange 1995). The fortuitous comparison was between the first year of study at Amchitka when ecological conditions were seemingly normal, and the second year of study when an influx of spawning lumpsuckers from the oceanic realm subsidized the sea otter's diet during late winter/early spring (Watt et al. in press). In addition, the sea otter population at Amchitka was in the early phase of a decline when our field work began (Estes et al. 1998). The population decline did not appear induced by starvation, and current evidence suggests killer whale predation as the cause (Estes et al. 1998). The similar life history shifts seen in these two contrasts (Amchitka vs Kodiak, and Amchitka through time) strongly suggests that the shifts were responses to variation in the degree to which resources were limiting (as opposed to other habitat differences between Amchitka and Kodiak).

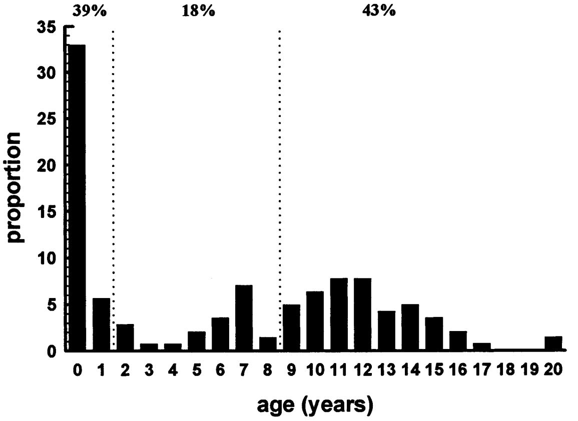

Fig. 6. Age distribution of sea otters found dead at Amchitka Island, Alaska from 1992 to 1994 ($n = 143$). Percentages between the vertical lines indicate the relative number of young, prime-age, and old animals.

Male and female sea otters of all ages were longer and heavier at Kodiak than they were at Amchitka. Total length likely has a genetic component of control, but may also indicate conditions during development. Nonetheless, M/L ratios should reflect current nutritional state, and were greater at Kodiak than they were at Amchitka (particularly for females). This suggests that Kodiak otters not only grew more rapidly, but were in better condition. Choquenot (1991) found a similar pattern when comparing a food-limited and non-food-limited population of feral donkeys (*Equus asinus*). This pattern is also evident in the sea otter M/L data collected by Kenyon (1969). In the early 1960s sea otters at Amchitka (an equilibrium population even then) had much lower M/L ratios than otters from the Shumagin Islands (then a growing population). Bodkin et al. (2000) found mean weights of sea otters declined over a 10-yr period before a resource related equilibration of the sea otter population at Bering Island, Russia. The fact that M/L ratios of very young animals

Table 3. Frequency distribution of 81 pup births and 61 pup separations for pups born to marked females at Amchitka Island from 1992 to 1994 (years pooled), and ratios of small pups to independent animals during monthly sea otter surveys during the same time period.

Month	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Births	5	6	8	3	18	12	8	9	2	4	3	3
Separations	1	8	0	1	3	0	6	9	2	13	7	10
Ratio	0.02	0.06	–	0.09	0.14	–	0.26	0.23	0.19	0.01	0.03	0.08

were similar for Amchitka and Kodiak, and diverged as they grew older (Fig. 2) strengthens the argument that these are environmentally induced differences as opposed to genetic. The higher M/L ratios of adult females in 1993 and the increases observed for the few individuals measured in both 1992 and 1993 at Amchitka suggest that the episodic appearance of lumpsuckers (Watt et al. in press) improved the general condition of the population.

Improved condition may lead to improved survival, particularly for young and old animals that may be most sensitive to late winter nutritional stress (Kenyon 1969). The paucity of fresh carcasses recovered at Amchitka during the late winter/early spring periods of 1993 and 1994, compared with earlier studies at Amchitka Island (Kenyon 1969, Estes 1977) suggests that starvation-induced mortality was comparatively low during our study. These various findings indicate differences in food availability between food-limited and growing populations have a direct influence on the sea otters' body condition.

Our findings also demonstrate the nature of life history and demographic responses to variation in food resource limitation. While some individual differences in gestation were evident here and in other locations (i.e., some females tended to have shorter or longer than average gestation periods; Riedman et al. 1994) the slight difference in mean gestation period between Kodiak and Amchitka is likely the result of imprecise estimates rather than inherent biological differences between populations. No differences in age-specific birth rates were evident between Amchitka and Kodiak (Fig. 3). Female reproductive rates and gestation periods were also similar to those reported for sea otter populations in California and Prince William Sound (Bodkin et al. 1993, Jameson and Johnson 1993, Riedman et al. 1994). These collective findings show that reproductive schedules in the sea otter are largely invariant across populations and thus unresponsive to changes in population status or food availability. However, we have argued that sea otters at Amchitka had been recently released from food-limitation at the time of our study. Whether or not reproductive suppression occurs under extreme food limitation remains to be determined. Extended birth intervals observed for females in the poorest condition suggest some amount of reproductive suppression may occur.

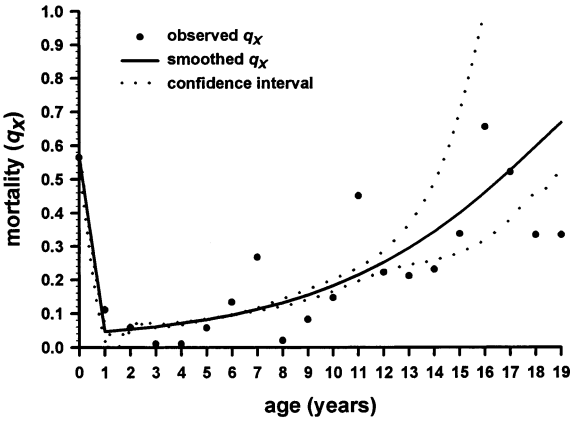

Fig. 7. q_x curve for sea otters at Amchitka Island, Alaska, based on the age distribution of beach-cast carcasses. Survival to age 1 estimated from the weaning success of pups born to radio-instrumented adult females. q_x curve computed as non-linear regression fit to mean values for each age-class (closed circles).

In contrast with the sea otter's rigid reproductive schedule, rates and patterns of pup survival varied considerably between Kodiak and Amchitka. Less than half the pups born to marked females at Amchitka survived to weaning whereas at Kodiak $>80\%$ survived. The fact that many of our marked females at Kodiak were young, inexperienced mothers makes this difference even more striking. The data gathered at Amchitka also describe a relationship between body condition and preweaning survival rates, and though we based this function entirely on Amchitka data, the predicted outcome for Kodiak agreed with the observed (logistic regression in Fig. 4). This relationship may be explained by the need for females to dramatically decrease feeding activity during the first weeks post-partum (Gelatt 1996). The pup relies entirely on its mother to be kept warm and dry as she carries the pup on her chest or hauls out for extended periods. Presumably females in poor condition cannot afford to restrict foraging time to the same degree as females with larger fat reserves, thus decreasing their attentiveness and subjecting the pup to longer periods in the water. The expected result would be decreased pup survival early in dependency, the time when most preweaning pup mortality occurs.

The seasonal decline in neonate survival at Amchitka (lowest in winter) may also be related to poor female condition. Winter storms and reduced temperatures would dictate even greater feeding restrictions and more attentive pup care by the female. Such reduced feeding and increased pup care may not be possible with limited fat stores. This would lead to a seasonality of births as females losing pups in early to mid-winter come into estrous and breed soon afterwards, thus giving birth to another pup about six months later during the late spring/early summer pupping peak. Higher preweaning survival in these pups and the roughly one year length of a successful reproductive cycle would maintain this peak. In support of this explanation, birth rates at Kodiak were seasonally uniform, presumably because of improved female body condition.

Many pups that weaned successfully at Amchitka likely died shortly thereafter. Zero- and 1-yr class animals comprised 40% of the total number of beach-cast carcasses suggesting that mortality for recently weaned animals at Amchitka had been high just before our study. During our study only two of 11 radio-tagged weanlings were known to survive their first year of independence. In contrast, few beach-cast carcasses were found at Kodiak during late winter/early spring which is generally the period of peak sea otter mortality (Kenyon 1969), and most known causes of death were human-related (DeGange and Vacca 1989, Monson and DeGange 1995). Collectively these results indicate that most sea otter pups born into equilibrium density populations die during their first year, and that this is the principal demographic mechanism of population regulation. In addition, first year mortality occurs in two peaks; a post-partum peak related to the female's age and condition, and a postweaning peak likely related to the severity of winter weather and the weanlings ability to acquire adequate food resources.

A predicted consequence of this tactic, when coupled with a time-varying environment, is the departure from a stable age distribution. Support for this prediction is found in the age distribution of beach-cast carcasses at Amchitka (Fig. 6). The depressed number of 8- and 13-yr-olds, and relatively large number of 7-yr-olds in our samples, may be a consequence of episodic bad and good years. Similar patterns were seen in the age structure of sea otter carcasses collected in Prince William Sound after the *Exxon Valdez* oil spill, which provided a uniquely unbiased sample of age distribution from a living population (Udevitz and Ballachey 1998). However, if we assume juvenile survival varies around some mean, then over time we may expect the age structure to vary around a "stationary distribution" (Caswell 1989: 208–212).

Life history tactics

When considered on a macroevolutionary time scale, the sea otter is a recent expatriate from land or fresh water into the sea. As such, a mix of phylogenetic constraints bequeathed from its terrestrial or freshwater ancestors and selective pressures imposed by life in the sea has molded its life history. These qualities, when viewed against a background of life history variation among terrestrial, semi-aquatic, and fully marine species, provide insight into the nature of life history adaptations associated with the evolution of marine living in mammals.

If phylogenetic constraints have caused the sea otters' reproductive inflexibility, then one would expect to see this and other reproductive characteristics conserved among closely related extant taxa (i.e., other species of mustelids and particularly other lutrines). The diversity of reproductive patterns among these species (Table 4) argues against phylogenetic inertia. For instance, there is considerable variation in the length of diapause in mustelids and the extent to which lutrine species breed seasonally. Sea otters are remarkably different from their closest living relatives in such life history characters as litter size, state of development at birth, and rate of post-partum development (Estes 1989). A striking feature of this comparison among species is the relation of litter size and litter mass. Maximum reported litter size for the 26 species of mustelids listed in Table 4 ranges from one to 18, and all species except sea otters produce multiple-young litters. In this life history character, sea otters are more like pinnipeds and cetaceans, all of which invariably have single-young pregnancies. For both the mustelids and pinnipeds, mean litter mass increases with mean adult body mass (Fig. 8). However, whereas the sea otter's adult body mass lies near the upper end of the size range for mustelids and the lower end of the size range for pinnipeds, the sea otter appears much more like a pinniped (with whom it shares a common environment) than other mustelids (with whom it shares a closer common ancestor; Fig. 8). These patterns seem to reflect extreme lability in the genetic control of life history on the one hand, and strong selection in marine mammals for large, precocial young on the other. If this interpretation is correct, then the sea otter's response to environmental fluctuations also helps clarify the adaptive significance of its life history patterns, especially when viewed from the perspective of life history theory.

If the sea otter's life history were largely a product of selection imposed by long periods of food limitation around carrying capacity, then the species should perform as a classic K-strategist (Stearns 1976). Although many species, including sea otters, fit some predictions of this model (Estes 1979, 1989), there is growing evidence that reproductive success in numerous marine birds and mammals varies in response to episodic environmental change. A well known example is the widespread detrimental impact of recent El Niño events (Trillmich and Ono 1991). Due to their longevity, individuals of many marine bird and mammal species might expect to encounter one or more such events during their lives, although exactly when any particular event would occur is unpredictable. The episodic nature and strong influence of lumpsucker abundance on sea otters, while beneficial as opposed to detrimental, is similar in this regard. Because of the rapid and seemingly unpredictable nature (relative to generation time) of these large-scale environmental changes, species that successfully exploit them must do so by either storing energy (e.g., pinnipeds) or reproducing when conditions are favorable. Sea otters cannot store significant amounts of energy, but their uniform birth rates and tendency to come into estrus immediately after the loss of a pup are life history features that make the sea otter well-suited for a rapid response. If individuals waited for optimal times to become pregnant, give birth and successfully wean their pups, many of these brief but propitious events would come and go before they could exploit them.

Table 4. Comparisons of life history traits for 24 species of mustelids (from Nowak 1991 and Parker 1990).

Species	Litter size	Mean litter weight (g)	Lactation	Females mature	Life expectance
Mustela nivalis (least weasel)	1 to 7 (5)	8.0	24 d	120 d	1 yr
Mustela erminea (ermine)	4 to 13 (6)	13.8	30 d	60–90 d	3–4 (7) yr
Mustela frenata (long-tailed weasel)	3 to 9 (6)	18.6	25 d	90–120 d	?
Mustela vision (American mink)	2 to 10 (5)	.	40 d	12 mo	10 yr
Mustela putorius (European polecat)	2 to 12 (5)	47.5	30 d	1 to 2 yr	5–6 (14) yr
Mustela putorius furo (domestic ferret)	2 to 12 (5)	.	30 d	1 to 2 yr	5–6 (14) yr
Mustela eversmanni (steppe polecat)	4 to 18 (9)	45.0	45 d	9 mo	?
Martes martes (European pine marten)	2 to 6 (3)	90.0	6–7 wk	14–39 mo	max 17 yr
Martes zibellina (sable)	1 to 5 (3)	97.5	7 wk	15–39 mo	max 15 yr
Martes americana (American pine marten)	1 to 5 (3)	84.0	6 wk	15–39 mo	max 17 yr
Martes pennanti (fisher)	1 to 4 (2.5)	100.0	8–10 wk	12 mo	10 yr
Eira barbara (tayra)	2 or 3 (2.5)	207.5	8–12 wk	?	max 18 yr
Gulo gulo (wolverine)	1 to 5 (3)	285.0	8–10 wk	2–3 yr	max 17 yr
Meles meles (Old World badger)	2 to 6 (3.5)	280.0	10 wk	1 yr	max 16 yr
Taxidea taxus (American badger)	1 to 7 (3)	282.0	6 wk	120 d to 1 yr	14 yr
Spilogal putorius (spotted skunk) east	2 to 9 (5)	101.3	54 d	1 yr	max 10 yr
Spilogal putorius (spotted skunk) west	1 to 6 (4.5)	.	55 d	6 mo	max 10 yr
Mephitis mephitis (striped skunk)	1 to 10 (4.5)	135.0	8–10 wk	1 yr	6 yr (12)
Lutra lutra (European otter) north	1 to 4 (2)	260.0	12–16 wk	2 to 3 yr	max 22 yr
Lutra lutra (European otter) south	1 to 4 (3)	.	12–16 wk	2 to 3 yr	max 22 yr
Loutra canadensis (river otter)	2 to 4 (2.7)	351.0	12–16 wk	2 to 3 yr	max 23 yr
Loutra felina (Chungungo)	2	.	.	.	.
Aonyx cinerea (Oriental small-clawed otter)	1 to 6 (2)	.	10–12 wk	?	?
Aonyx capensis (Cape clawless otter)	2 to 5 (2)	.	?	?	11 yr
Pteronura brasiliensis (giant otter)	1 to 5 (2)	400.0	3–4 mo	?	max 13 yr
Enhydra lutris (sea otter)	1	1990.0	4–8 mo	2 to 5 yr	20 yr

Stearns (1976) has termed such life history tactics in response to environmental uncertainty as "bet-hedging". Bet-hedging models predict that, for a species living in a fluctuating environment in which adult survival is high, the optimal strategy includes low reproductive effort (Schaffer 1974, Wilbur et al. 1974, Stearns 1976, Goodman 1979). In sea otters most unsuccessful reproductive attempts end early in dependency, thus suggesting low reproductive effort or "reproductive restraint" (sensu Curio 1983). That is, the female may provide less to its offspring than is physiologically necessary to increase her own survival and subsequent reproductive success. Viewed from this perspective, variation in preweaning pup survival may be a facultative life history trait under female control.

Many differences between sea otters and their closest terrestrial or freshwater-living relatives appear to be adaptive responses to life in the sea. Litter size in sea otters is nearly always one, even when resources are abundant. They share this quality with all other fully marine mammals (i.e., pinnipeds, cetaceans, and sireneans) but with none of their closest relatives (i.e., other mustelids). The production of a large, precocial pup is likely a prerequisite for survival in the harsh marine environment. Interestingly, coastal living European otters (*Lutra lutra*) tend to have smaller litters than those living in fresh water habitats (Kruuk 1995) suggesting a strategy with more "K-ness" in response to the relative stability of the ocean environment as perceived by a river otter (Begon and Mortimer 1986: 164–172). This further suggests a possible evolutionary route for invasion of the marine environment by lutrines where the presumable facultative adaptation of the ancestor becomes necessary (i.e., obligatory) for the success of the new species.

Life history theory has long predicted departures from classic r- and K-strategies depending on trophic and environmental interactions (Wilbur et al. 1974, Stearns 1976, Goodman 1979, Begon and Mortimer 1986). The common life history patterns that occur among sea otters, other marine mammals, and marine birds, and the divergence of these characters from those of classical K-strategists, suggest that unpredictable variation (as perceived by these generally long-lived organisms) has influenced species living in the marine realm as much as the predictable seasonal changes faced by many terrestrial vertebrates. This suggests further that the diversifying influences of environmental change can act relatively quickly in vertebrate life history evolution.

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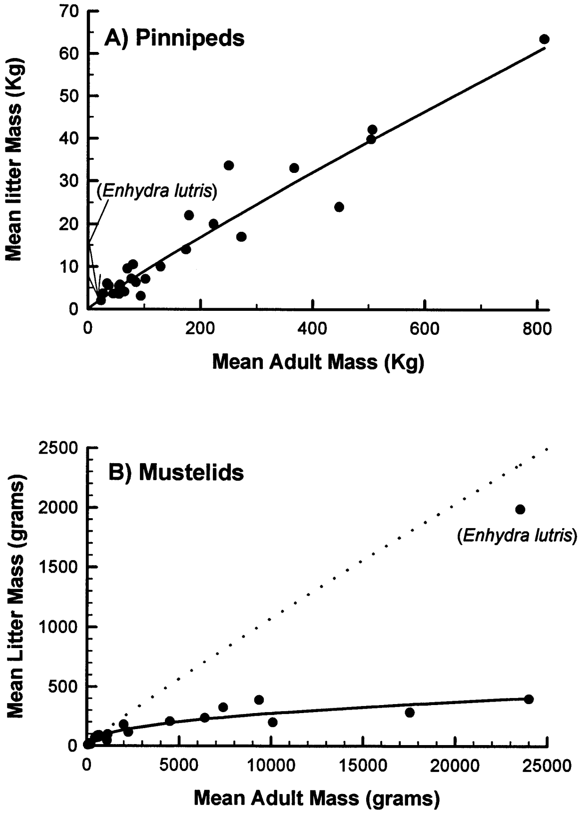

Fig. 8. A. Allometric relationship (non-linear regression) between mean adult female mass and mean pup mass for 26 species of pinnipeds (data from Lee et al. 1991). Solid line is best fit to all data except *Enhydra lutris* ($Y = aM^b$; $a = 0.23$ [std err = 0.20], $b = 0.92$ [std err = 0.7], $R^2 = 0.92$, $F = 274$, $P < 0.0001$; the *Enhydra lutris* data point falls within the 95% confidence limits). B. Allometric relationship (non-linear regression) between mean adult female mass and mean litter mass (mean litter size × mean pup mass) for 19 species of Mustelidae (Table 4; data from Parker 1990, and Nowak 1991). Solid line is best fit to all data except *Enhydra lutris* ($Y = aM^b$; $a = 4.82$ [std err = 2.7], $b = 0.44$ [std err = 0.06], $R^2 = 0.84$, $F = 81.8$, $P < 0.0001$; the *Enhydra lutris* data point falls outside the 95% confidence limits). Dotted line is the relationship found for pinnipeds.

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