

Patterns of growth and body condition in sea otters from the Aleutian archipelago before and after the recent population decline

K. L. LAIDRE*, J. A. ESTES*†‡, M. T. TINKER*, J. BODKIN§,
D. MONSON§ and K. SCHNEIDER¶

*Department of Ecology and Evolutionary Biology, Long Marine Laboratory, University of California, Santa Cruz, CA 95060, USA; †USGS Western Ecological Research Center, Sacramento, CA 95826, USA; ‡Alaska SeaLife Center, Seward, AK 99664, USA; §USGS Alaska Science Center, Biological Sciences Division, 1011 E. Tudor Road, Anchorage, AK 99503, USA; ¶PO Box 15214, Fritz Creek, AK 99603, USA

Summary

1. Growth models for body mass and length were fitted to data collected from 1842 sea otters *Enhydra lutris* shot or live-captured throughout south-west Alaska between 1967 and 2004. Growth curves were constructed for each of two main year groups: 1967–71 when the population was at or near carrying capacity and 1992–97 when the population was in steep decline. Analyses of data collected from animals caught during 2004, when the population density was very low, were precluded by a small sample size and consequently only examined incidentally to the main growth curves.

2. Growth curves demonstrated a significant increase in body mass and body length at age in the 1990s. Asymptotic values of body mass were 12–18% higher in the 1990s than in the 1960s/70s, and asymptotic values for body length were 10–11% higher between the same periods. Data collected in 2004 suggest a continued increase in body size, with nearly all data points for mass and length falling significantly above the 1990s growth curves.

3. In addition to larger asymptotic values for mass and length, the rate of growth towards asymptotic values was more rapid in the 1990s than in the 1960s/70s: sea otters reached 95% of asymptotic body mass and body length 1–2 years earlier in the 1990s.

4. Body condition (as measured by the log mass/log length ratio) was significantly greater in males than in females. There was also an increasing trend from the 1960s/70s through 2004 despite much year-to-year variation.

5. Population age structures differed significantly between the 1960s/70s and the 1990s with the latter distribution skewed toward younger age classes (indicating an altered l_x function) suggesting almost complete relaxation of age-dependent mortality patterns (i.e. those typical of food-limited populations).

6. This study spanned a period of time over which the population status of sea otters in the Aleutian archipelago declined precipitously from levels at or near equilibrium densities at some islands in the 1960s/70s to < 5% of estimated carrying capacity by the late 1990s. The results of this study indicate an improved overall health of sea otters over the period of decline and suggest that limited nutritional resources were not the cause of the observed reduced population abundance. Our findings are consistent with the hypothesis that the decline was caused by increased killer whale predation.

Key-words: age-independent mortality, age structure, Alaska, body condition, growth curves.

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Introduction

The concepts of population limitation and regulation are not new to ecology (Allee *et al.* 1949). Control of population dynamics and population status can change as feedback processes change in response to environmental conditions and/or population density (Berryman 2004). Body condition – e.g. size at age or relative energy stores – is often used as a proxy for fitness and can inform demographic and ecological inferences (Trites & Bigg 1992; Calkins, Becker & Pitcher 1998; Guniet *et al.* 1998; McMahon, Burton & Bester 2000; Bowen *et al.* 2003), such as population status relative to environmental carrying capacity or conditions of the ecosystem (Fowler & Siniff 1992). However, robust longitudinal studies of body condition in free-ranging mammals are met with steep requirements, such as large sample sizes at the individual-level over multiple generations during a period of population fluctuation. Thus, a relative paucity of such studies exists in the ecological literature.

Sea otters *Enhydra lutris* in the Aleutian archipelago have recently experienced one of the most widespread and precipitous population declines of any mammalian carnivore in recorded history (Doroff *et al.* 2003). The decline began in the late 1980s or early 1990s and is ongoing. At some islands within this region, declines of 92–99% were observed from starting levels close to equilibrium density (Doroff *et al.* 2003; Estes *et al.* 2005). The weight of available evidence indicates that this decline was driven largely or exclusively by increased killer whale *Orcinus orca* predation (Estes *et al.* 1998, 2004), which Springer *et al.* (2003) hypothesized occurred as a result of changes in the prey base of other sympatric marine mammal species inhabiting the North Pacific Ocean.

As a result of their substantial individual energy requirements (Costa & Kooyman 1982) and high population densities (Estes 1989), sea otters strongly depress their prey populations (Estes & VanBlaricom 1985) and food availability is often suspected to be the principal driver of population change (Kenyon 1969; Estes, Jameson & Rhode 1982; Bodkin, Burdin, & Ryazanov 2000). Given the suggested links between resource availability, fitness and demography in marine mammals (Boyd 1984; Costa, Croxall & Duck 1989; Lunn & Boyd 1993; Calkins *et al.* 1998; Guniet *et al.* 1998; Monson *et al.* 2000; Soto, Trites & Arias-Schreiber 2004), the body condition of sea otters should serve as an objective and sensitive index of population status with respect to food availability.

The objective of our analysis was to describe quantitatively changes in body condition of Aleutian sea otters between 1967 and 2004, a period over which the population in western Alaska declined between one and two orders of magnitude (Estes *et al.* 2005). If the principal factor regulating population growth switched from resource limitation to predation (or any form of density-independent mortality), we would predict that

per capita prey availability, and thus body condition, should increase over the period of this decline. The relative merits of four growth models were compared and used to describe the growth of male and female sea otters and examine temporal trends in maximum body size and rates of growth. Changes in age structure were compared between the same periods by contrasting observed age distributions with those expected under alternative scenarios of age- and cause-specific mortality.

The availability of an expansive data set spanning over three decades for a population that has fluctuated across the full range of possible densities provides an unparalleled opportunity to explore the relationship between age-specific physiological indices of body condition and population status. This well-chronicled example may provide a model by which the general causes of population change in other mammalian carnivores, and even less closely related taxa, can be assessed through contrasts of body condition and population structure over space and time.

Materials and methods

DATA COLLECTION

Body mass and body length were measured from sea otters in the Aleutian Islands between 1967 and 2004. Data were obtained from 1643 sea otters harvested by the Alaska Department of Fish and Game from April–August of 1967–71 (referred to hereafter as the 1960s/70s) in waters near Amchitka, Adak, Kanaga, Tanaga and the Delarof islands (Fig. 1). Mass and length data were recorded for each individual, usually immediately after death but in some cases up to a few hours later. Between 1992 and 1997 (referred to hereafter as the 1990s) and in 2004, body mass and length were measured from 198 sea otters live-captured between May and August in waters near Adak, Amchitka, Attu, Kanaga, Kiska and the Semichi islands (Fig. 1). Sea otters were captured using floating gill nets or Wilson traps operated by rebreather-equipped divers (Ames *et al.* 1983; Benz & Britton 1995) and anaesthetized with fentanyl and diazepam (Monson, McCormik & Ballachey 2001). After immobilization, standard body measurements (mass and length) were collected from each individual. Anaesthesia was reversed with the narcotic antagonist naltrexone.

Body mass (kg) was measured with a 50 kg spring scale and rounded to the nearest kilogram. Between 1967 and 1971, body length was measured as the curvilinear (CL) distance from the tip of the nose to the tip of the tail with the animal on the dorsal surface. In the 1990s and in 2004, body length was measured as the straight-line (SL) distance between the tip of the nose and the tip of the tail while the animal was fully stretched on its back. Curvilinear lengths were corrected to standard lengths using data for six sea otters from which both types of length were measured. Variance in asymptotic length estimates for the 1960s/70s

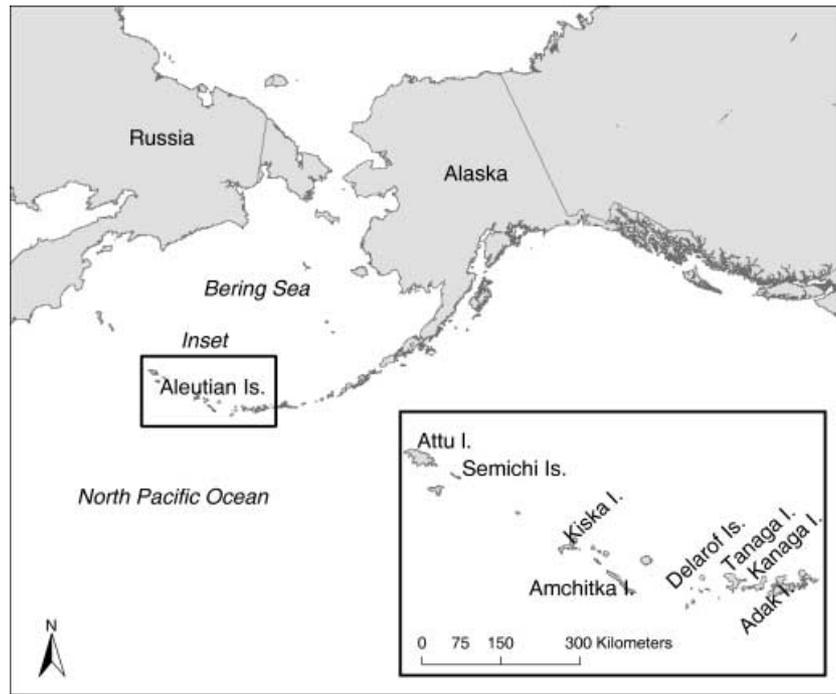


Fig. 1. Map of Aleutian Islands, Alaska. Inset shows the location of specific islands mentioned in the text where sea otters were harvested or live captured.

was adjusted upwards based on the estimated variance from the correction factor, which was the sum of the variance among individuals and the variance in measurement error.

Tooth ages (Bodkin *et al.* 1997) from extracted premolars were available for 100% of sea otters shot between 1967 and 1971 and 68% of those live captured between 1992 and 2004. Age was also estimated for all animals in the 1990s and 2004 based on a physical examination of tooth wear, head grizzle, and overall physical characteristics. Estimated age correlated well with tooth age when both parameters were available and the best fit to the relationship was estimated with a curvilinear model (Fig. 2). Estimated ages were adjusted based on this relationship and the two ages were combined into a single field for growth models.

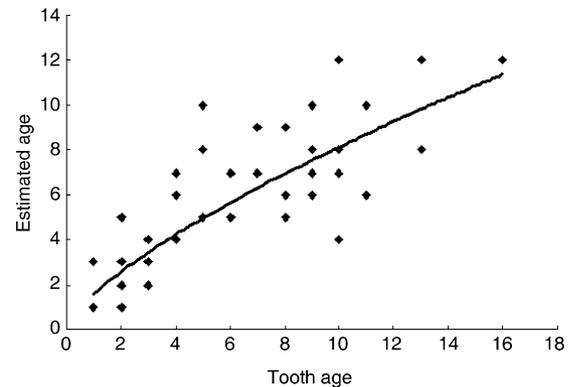


Fig. 2. Regression model of tooth age (Matson age) and estimated age (based on tooth wear) for sea otters in the Aleutian Islands, Alaska, captured in 1995 and 1997. Curvilinear model fit as $y = 3.248 * x^{0.4877} - 1.764$ and $R^2 = 0.6723$.

DATA ANALYSIS

Analysis of growth in mass and length was conducted using sea otters ≥ 1 year old (weaned juveniles) to remove any bias between time periods introduced by variability in ages assigned to dependent pups. Animals aged as 0 or 1 year old in the 1960s/70s were eliminated from the analysis due to speculation that the presumed age at weaning was different in the earlier period from what it is now known to be. Age frequency distributions were tested for significance between time periods with a two sample Kolmogorov–Smirnov goodness of fit test (significance at $P < 0.05$).

Because sea otters are bimaturistic and sexually dimorphic (Estes 1989), each sex was analysed separately. Growth curves were constructed for sex-specific

body mass and body length for each of two year groups: 1967–71, when the population was at or near carrying capacity (Kenyon 1969; Estes 1990), and 1992–97, when the population was in steep decline (Doroff *et al.* 2003). In some cases, measures or estimates of both length and mass were not available for an individual, thus models had differing sample sizes. Growth models were fit using the nonlinear least squares regression feature (NLM) in S-PLUS version 6.1 (Insightful Inc.). Four mathematical models (von Bertalanffy, Gompertz, modified Gompertz, and Logistic) were explored to estimate growth in body length and body mass (Table 1). As all of these models have the same number of parameters, the best fit for subsequent analysis was determined from the minimum residual sum of squares. Significant

Table 1. Growth models fit to size (body length and body mass) at age (t) data for male and female sea otters during each of two time periods. Parameter A is asymptotic size, in the von Bertalanffy equation k determines the rate at which growth decreases and t_0 is the time at which the curve becomes tangent to the time axis. In other equations, a is the instantaneous rate of growth (or the instantaneous rate of growth at inflection in the Gompertz model) and b is the time at which the absolute growth rate begins to decrease

Model	Reference	Equation
von Bertalanffy	von Bertalanffy (1938) Ricker (1979)	$A_{\infty}(1 - e^{-k(t-t_0)})$
von Bertalanffy	Von Bertalanffy (1938) Ricker (1979)	$A_{\infty}(1 - e^{-k(t-t_0)})^3$
Modified Gompertz	Kappenman (1981)	$A_{\infty}(1 - e^{-ae^{bt}})$
Gompertz	Ricker (1979)	$A_{\infty}e^{-(a/b)e^{-bt}}$
Logistic	Ricker (1979)	$A_{\infty}/(1 + ae^{-bt})$

differences in model parameters between time periods were evaluated using a t -test for unequal sample sizes and unequal variances. The age at which sea otters reached 95% of asymptotic size was determined for both sexes and time periods.

Data collected during live captures in 2004 were examined relative to the two main time periods, however, small sample sizes precluded comprehensive comparisons of growth curves. Differences were assessed by examining the distribution of the individual deviations for the 2004 data around the 1990s growth curve, and comparing these residuals with the residuals from the 1990s data set using a Kruskal–Wallis one-way ANOVA with significance set at 0.05.

We assumed that the ratio of body mass to length was a reasonable metric of relative body condition in sea otters (Monson *et al.* 2000). This index was examined for differences in average body condition between time periods. A locally weighted regression (LOWESS) was used both to remove the potentially confounding effect of age (younger animals and very old animals tend to have a lower mass to length ratio) and because shifts in the age composition over time were suspected. A robust kernel-weighting method was used to fit the LOWESS-smoothed, polynomial regression of the $\log(\text{weight})/\log(\text{length})$ ratio against age. Residuals from this relationship were used as an age-independent index of relative body condition (Silva 1998; Green 2001). A two-factor ANOVA was used to test for the effects of sex and time period (1960s/70s, 1990s and 2004) and an interaction. The 1960s/70s and 1990s periods were then tested with a nested ANOVA (years nested within periods) to examine year-to-year differences. Residuals were examined prior to all analyses to ensure that assumptions of normality and heterogeneity of variance were met and that the effect of age was entirely removed from the body condition index using the LOWESS smoothing method.

POST-MORTEM EFFECTS

Concerns about the possibility of systematic differences in body length between living and fresh-dead sea otters led to a post-mortem calibration based on data collected in central California, as matching sets of measurements from living and dead animals in western

Alaska were not available. Between 1995 and 2000, 220 body length measurements were obtained from 71 live-captured sea otters (41 female, 30 male) and 149 beach-cast carcasses (65 female, 85 male) in central California at various sites along the coast between Santa Cruz and Morro Bay. Age distributions within data sets were similar and ranged from 1- to 15-year-old animals. Separate growth curves were fit to standard body length measurements from live and dead animals to test for post-mortem effects on body length. Analyses conducted on dead sea otters were limited to fresh carcasses (collected within 1–2 days after death) obtained in the same geographical areas and time periods as the live captures to ensure comparability between the data. Body mass was not examined for post-mortem effects because diverse causes of death in the stranded carcasses would have confounded the analysis.

DEMOGRAPHIC ANALYSIS

Temporal changes in the age structure of a population, when combined with information on population growth rate (λ), provide a means of interpreting trends in age-specific vital rates (Eberhardt 1988; Udevitz & Ballachey 1998; Doak & Morris 1999). Owing to the likelihood of significant (but unquantifiable) age-based biases in the two databases (due to spatial segregation, juveniles were less likely to be captured in the 1990s or shot in 1960s/70s), it was not possible to formally fit demographic rates to the age-distribution data using maximum likelihood methods (e.g. Udevitz & Ballachey 1998). However, qualitative changes in age structure that would be expected under different scenarios of age-specific mortality could be predicted and compared with the observed differences between the 1960s/70s and 1990s age distributions. The rate of population decline for the western Aleutians was assumed to be approximately 15% per year over the period 1987–95 (Doroff *et al.* 2003). The population was assumed to be approximately stable ($\lambda = 1$) and at carrying capacity prior to the decline. Typically, growth in sea otter populations is limited not by fecundity but by age-dependent mortality. In particular, populations at carrying capacity are characterized by low pre-weaning and juvenile survival, higher survival for prime-aged adults,

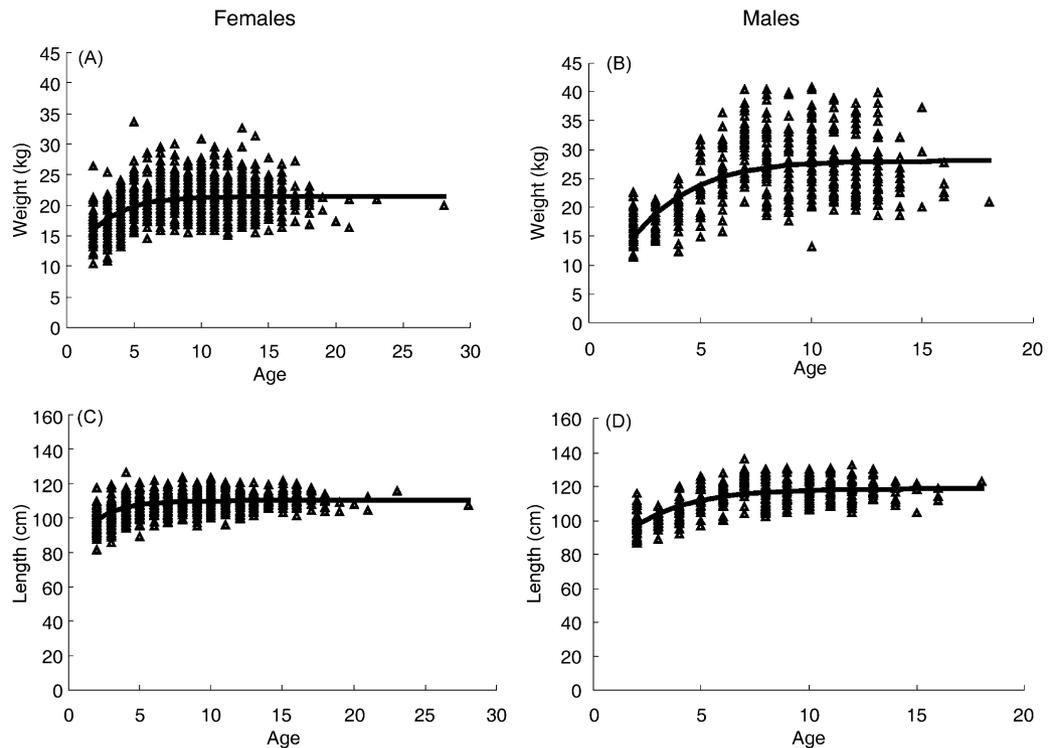


Fig. 3. Measured values and fitted curves for female body mass (A), male body mass (B) (in kg), female body length (C), and male body length (D) (in cm) between 1967 and 1971.

and low survival for aged adults (Monson *et al.* 2000). In contrast, mortality from killer whale predation appears to be age-independent (Estes *et al.* 1998). We evaluated the expected shifts in age distribution under three scenarios: (1) the observed decline was caused not by predation, but by an increase in age-dependent mortality (as might be expected due to starvation or nutritional stress); (2) the observed decline was caused by predation, and age-dependent mortality (i.e. from all causes other than predation) decreased gradually over the 8-year period as food became relatively more abundant; and (3) the observed decline was caused by predation, and age-dependent mortality decreased rapidly over the 8-year period.

The approach projected population dynamics and changes in population age structure using matrix multiplication (Caswell 2001). A two-sex, age-based Leslie matrix was constructed with a maximum age of 20 years following Gerber *et al.* (2004). All matrix transition rates were parameterized using age-specific fecundity and survival values for a carrying-capacity population in Alaska (Monson *et al.* 2000). The population vector was initialized using the algebraically derived stable age distribution (Caswell 2001) and then projected for 8 years. The resulting age distributions for each of the three scenarios were plotted and compared with the actual pre- and post-decline age distributions. For scenario 1, age-specific survival rates were adjusted to achieve a realized growth rate of $\lambda = 0.85$, assuming that the additional mortality exhibited

the same age-dependent patterns as the mortality required to reduce population growth from r_{\max} ($\lambda = 1.18$, Estes 1990; Monson & Degange 1995) to equilibrium ($\lambda = 1$). This adjustment resulted in substantial depression of pre-weaning and post-weaning juvenile survival, while prime-age adult survival was lowered to a lesser degree. For scenarios 2 and 3, survival rates were adjusted to achieve a realized growth rate of $\lambda = 0.85$, with the key difference being that additional mortality was partitioned equally among age classes as would be expected for killer whale predation. Under scenario 2, age-dependent mortality was relaxed by small increments each year, such that by 1995 the intrinsic rate of growth for the population (if all predation suddenly stopped) would be $\lambda = 1.08$. Under scenario 3, age-dependent mortality was relaxed by larger increments each year, such that by 1995 the intrinsic rate of growth for the population (if all predation suddenly stopped) would be $\lambda = 1.18$.

Results

In total, 1199 (1967–71) and 142 (1992–97) females and 444 (1967–71) and 56 (1992–97) males were used in the analysis. In 2004, nine females and two males were measured and examined with respect to the curves constructed for the two main time periods. A ratio of 0.85 standard length/curvilinear length (SE 0.018 including individual variation and measurement error) was developed to transform length data collected in the 1960s/

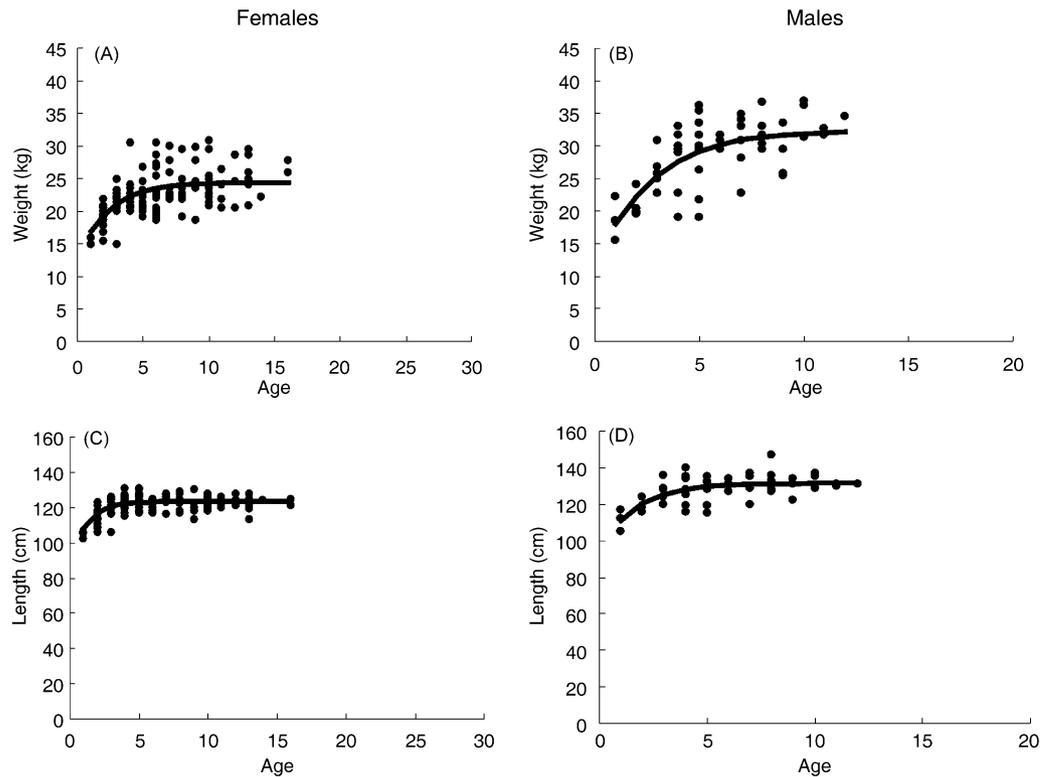


Fig. 4. Measured values and fitted curves for female body mass (A), male body mass (B) (in kg), female body length (C), and male body length (D) (in cm) between 1992 and 1997.

70s based on the overall mean of three to four replicate measures of both CL and SL from six otters.

MASS-AT-AGE MODELS

All growth models for body mass fit the data well and resulted in curves that were virtually indistinguishable (Table 1). We arbitrarily chose the von Bertalanffy model for all subsequent characterizations of growth. Maximum observed body mass was larger for male sea otters than females in all time periods. Growth curves demonstrated a significant increase in body mass at age for male and female sea otters between the 1960s/70s and the 1990s (Figs 3 and 4). In the 1960s/70s, asymptotic values (M_{∞}) for females and males were 21.4 kg (SE 0.14) and 28.1 kg (0.47 SE), respectively. These values had significantly increased in the 1990s by 3 kg for females ($P < 0.001$) and 4.2 kg for males ($P < 0.01$) (Table 2). Female sea otters reached 95% of M_{∞} at age 6 in the 1960s/70s and age 5 in the 1990s. Male sea otters reached 95% of M_{∞} at age 8 in the 1960s/70s and age 7 in the 1990s.

LENGTH-AT-AGE MODELS

Growth curves for body length followed the same pattern as those for body mass. Maximum observed length was larger for males than for females (Table 2). Asymptotic body length (L_{∞}) significantly increased for male and female sea otters from the 1960s/70s to the 1990s (Figs 3 and 4). In the 1960s/70s, female and male sea

otters were on average 110.0 cm (SE 2.4) and 118.7 cm long (SE 2.7), respectively. However, both male and female sea otters were on average 13 cm greater in length in the 1990s (approximate 10–11% increase, $P < 0.001$ for both sexes; Table 2). Growth in body length appeared to be more rapid during the 1990s for both sexes and estimates of k were significantly different for male sea otters ($P < 0.05$). In general and irrespective of temporal variability, growth in body length reached an asymptote at an earlier age than did growth in body mass. Female sea otters reached 95% of L_{∞} at age 4 in the 1960s/70s and age 3 in the 1990s. Male sea otters also reached 95% of L_{∞} at age 6 in the 1960s/1970s and age 4 in the 1990s.

2004 DATA

Morphometric data were collected from 11 live captured animals (nine female and two male) in August 2004. With one exception, all measures of body mass and length in 2004 were above the fitted von Bertalanffy growth curves for the 1990s data (Fig. 5). Distributions of deviations about the 1990s fitted growth curve differed significantly between the 1990s and 2004 for both body mass and body length. Deviations about the 1990s growth curves were significantly greater in 2004 for female body mass ($F_{1,148} = 12.21$, $P < 0.001$), female body length ($F_{1,148} = 14.5$, $P < 0.001$), and male body mass ($F_{1,56} = 6.99$, $P < 0.05$). Male body length was not significant; however, the small sample size of males in 2004 ($n = 2$) resulted in a test of low statistical power.

Table 2. Parameters of von Bertalanffy growth curves (with 1 SE) fitted to body mass (kg) and body length (cm) of male and female Alaska sea otters in each time period. Standard errors for asymptotic length in the 1960s/70s are adjusted upwards for the added variance from the length correction

	1967–71			1992–97		
	A_{∞}	k (year ⁻¹)	t_0 (year ⁻¹)	A_{∞}	k (year ⁻¹)	t_0 (year ⁻¹)
Body mass						
Male	28.1 (0.47)	0.44 (0.07)	-1.81 (0.66)	32.3 (1.26)	0.42 (0.13)	-3.12 (1.45)
Female	21.4 (0.14)	0.44 (0.05)	-3.4 (0.71)	24.4 (0.46)	0.45 (0.10)	-3.78 (1.25)
Body length						
Male	118.7 (2.67)	0.38 (0.05)	-2.51 (0.64)	131.5 (1.34)	0.61 (0.19)	-2.05 (1.06)
Female	110.03 (2.40)	0.53 (0.06)	-2.35 (0.52)	123.32 (0.52)	0.82 (0.16)	-1.55 (0.57)

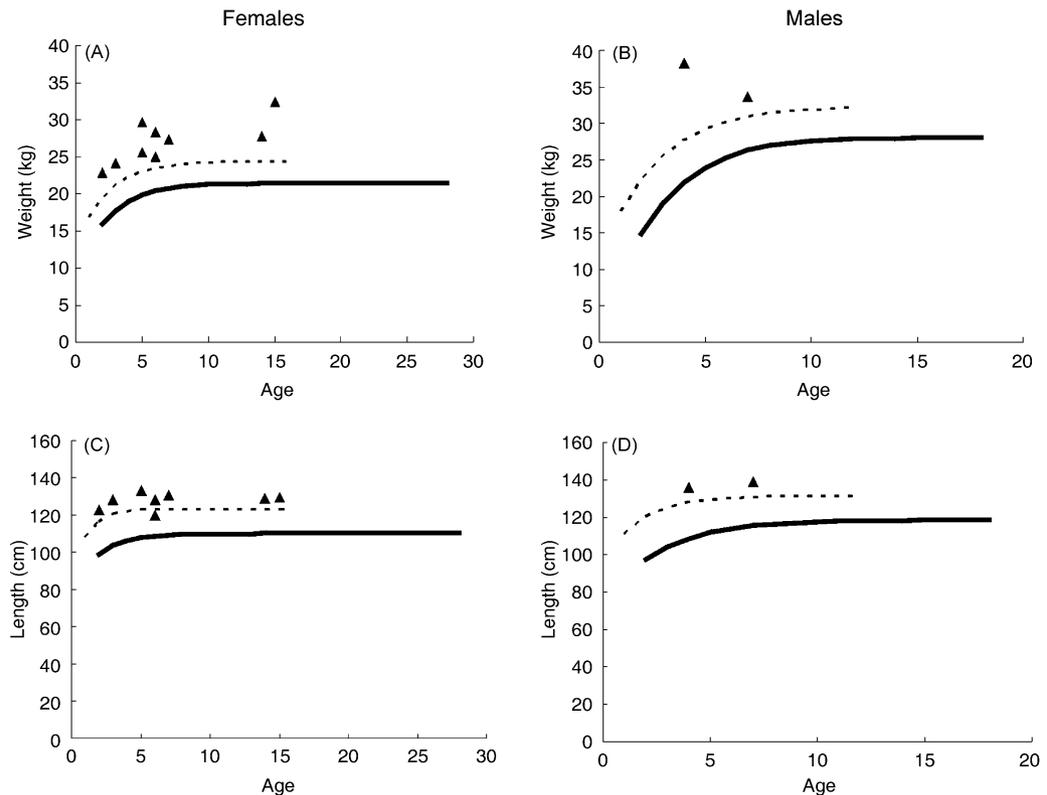


Fig. 5. Fitted curves for female (A) and male (B) sea otter body mass and female (C) and male (D) body length for periods 1967–71 (solid line) and 1992–97 (dashed line). Data collected in 2004 (black triangles) are shown on each graph.

MASS/LENGTH RATIOS

A LOWESS-smoothed, second-order polynomial regression of $\log(\text{weight})/\log(\text{length})$ against age for the entire data set resulted in a good fit (Fig. 6a). Residuals from this regression showed no relationship with age, were normally distributed, and exhibited similar variances for both sexes and all three time periods. Significant differences were found between males and females using the residuals as an index of body condition (males were consistently greater than females; $F_{1,1809} = 27.3$, $P < 0.001$) and there was no interaction between sex and time period ($F_{2,1809} = 1.2$, $P = 0.297$). Both males and females showed a consistent increase in body condition from the 1960/70s to the 1990s and from the 1990s to 2004 ($F_{2,1809} = 33.4$, $P < 0.001$; Fig. 6b). This

increasing trend in body condition was also evident after accounting for the significant year-to-year variation in body condition within the 1960s/70s and 1990s periods (time period effect $F_{1,6} = 37.8$, $P < 0.001$; years-within-time period effect $F_{6,1795} = 35.4$, $P < 0.001$). Mass-length ratio increased from 190.6 cm g^{-1} in the 1960s/70s (SE 0.7) to 216.9 cm g^{-1} in 2004 (SE 6.7) in adult females (13%), and from 227.6 cm g^{-1} in the 1960s/70s (SE 2.1) to 261.7 cm g^{-1} in 2004 (SE 19.1) in adult males (15%).

POST-MORTEM EFFECTS

The fact that animals from the 1960s/70s were shot, whereas those from the 1990s were live captured is a potentially confounding influence in the contrast of

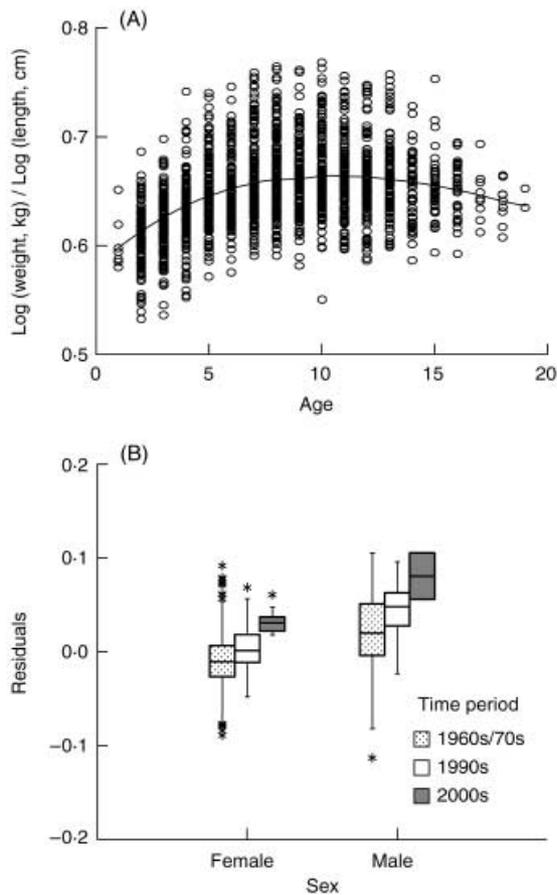


Fig. 6. Log-transformed mass/length ratios for sea otters plotted against age. The LOESS-smoothed, second-order polynomial regression curve is plotted over the raw data (A). Residuals from the regression were used as an age-independent index of body condition, and box-and-whisker plots of residual distributions are shown grouped by sex and by time period (B). Differences in body condition due to sex and time period were significant.

body size between these two periods. Data collected from sea otters live captured in central California and fresh sea otter carcasses from the same region and time period were evaluated for systematic differences in body length at age. All four growth models were fit to length at age data for male and female sea otters separately. The fitted growth curves for living and dead animals from California were virtually indistinguishable for both males and females (Fig. 7). Asymptotic length (L_{∞}) was 127.6 (SE 0.8) and 127.2 (SE 0.8) for dead vs. live females, and 118.7 (SE 1.0) and 118.4 (SE 1.2) for dead vs. live males. Relatively small sample sizes at young ages precluded definitive comparison of values for k ; however, estimates for this parameter were also very similar for living vs. dead animals.

AGE FREQUENCY DISTRIBUTIONS AND DEMOGRAPHY

Age-frequency distributions were significantly different between the 1960s/70s and 1990s for both male

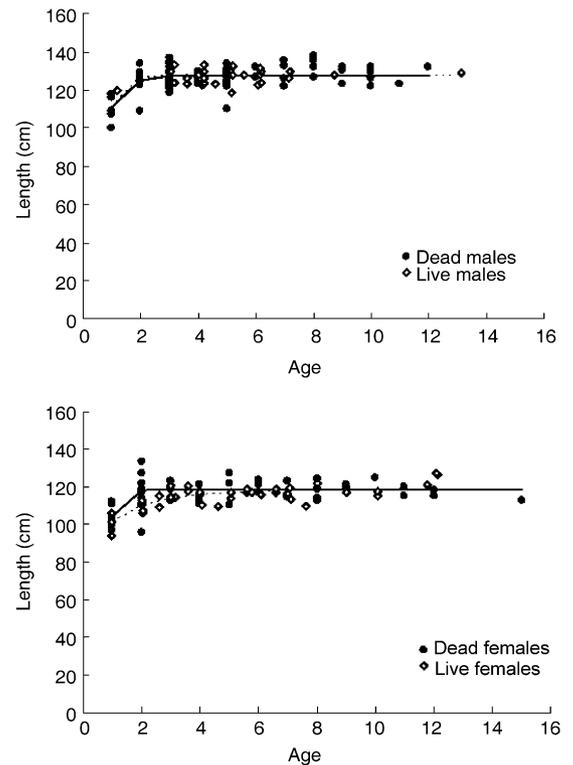


Fig. 7. Growth curve fits to body length (cm) data collected from beach-cast (dead) and live-captured sea otters in coastal California. The predicted fit to dead animals is shown with a solid line and the predicted fit to live animals is shown with a dashed line. Note minimal difference between fits to live and dead animals suggesting no effect of mortality on length measurements.

($KS = 0.7647$, $P < 0.001$) and female ($KS = 0.6522$, $P < 0.001$) sea otters. Differences were primarily evident as a truncated and left-skewed age distribution in the 1990s, with a higher proportion of young animals and fewer very old animals than in the 1960s/70s (Fig. 8a–d). Such a shift in age-structure occurring over the same period as a steep population decline is most consistent with the hypothetical scenario (2 and 3) of an increase in age-independent mortality accompanied by a reduction in age-dependent mortality (i.e. resulting in almost uniform survival probabilities across all age classes by 1995). In contrast, an increase in age-dependent mortality (sufficient to drive the observed rate of decline) would result in the opposite shift in age distribution (scenario 1) (Fig. 8a–d).

Discussion

Clearly, no mathematical growth model adequately describes the growth of an individual over the entire life cycle. However, by reducing the complex physical growth process into a few parameters that describe the nonlinear effect of age on size, meaningful comparisons can be made between sexes and time periods. The choice of growth model did not alter the results and all models fit the data almost equally well. This appears to

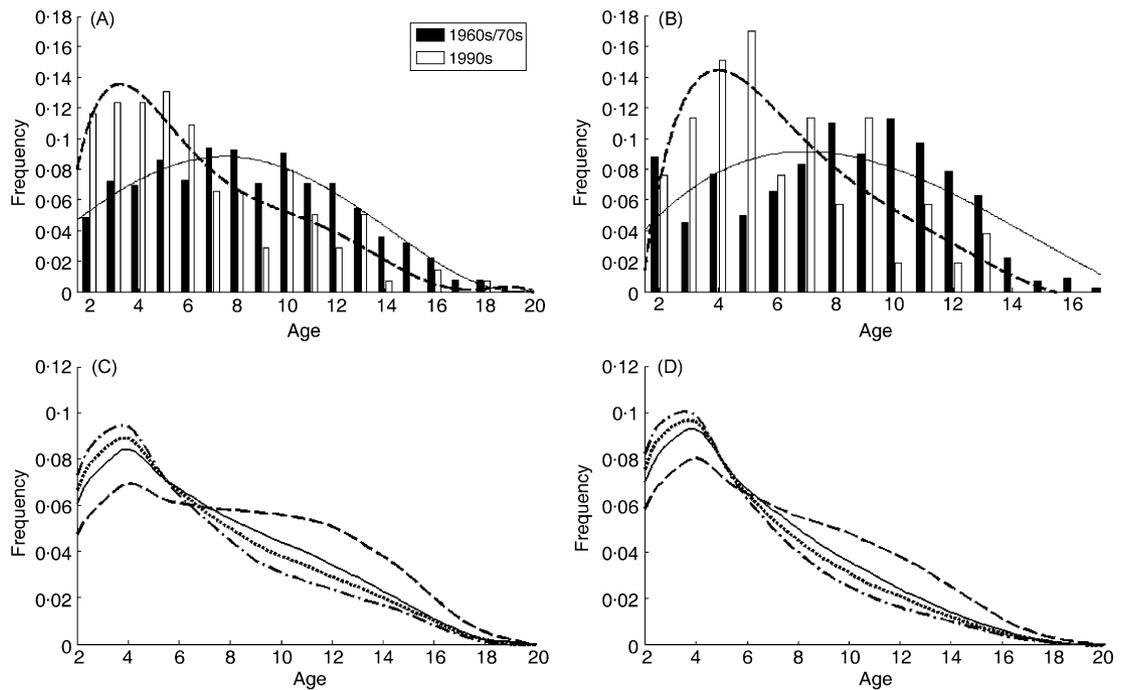


Fig. 8. Age-frequency distributions of sea otters used in this study are shown for females (A) and males (B). Data were collected between 1967 and 1997 from shot samples and live captures. Data collected in 2004 ($n = 11$ otters) are not shown. Expected changes in age distribution for females (C) and males (D) are also shown under three alternate demographic scenarios: (1) a decline due to increased age-dependent mortality, as would be expected for resource limitation (dashed lines); (2) a decline due to increased age-independent mortality, with gradual reduction of age-dependent mortality (dotted lines); (3) a decline due to increased age-independent mortality, with rapid reduction of age-dependent mortality (alternating dash-dot lines). The expected pre-decline age distributions (corresponding to $\lambda = 1.0$) are shown in (C) and (D) as solid lines for reference. Polynomial smoothing curves were fit to the raw data shown in (A) and (B) to facilitate visual comparison between observed and expected age distributions. The expected curves were adjusted to reflect representational bias against juveniles (we assumed a 0% chance of observing 1 year olds and a 50% chance of observing 2 year olds, relative to all other age classes).

be a consistent finding when fitting three-parameter growth curves to data from other mammalian species (Stewart 1994; Winship, Trites & Calkins 2001; Chabot & Stenson 2002).

In all models, length and mass of both sexes exhibited asymptotic growth with increasing age. Males reached greater body masses (on average 24–25% higher) and body lengths (7–8% higher) than females (Table 2). In the 1990s, 95% of growth in both sea otter body mass and body length was reached at earlier ages (on average 1–2 years) than in the 1960s/70s, suggesting animals approached asymptotic values more rapidly during the population decline than they did when the population was stable at or near equilibrium density. Male sea otter growth was, however, more sustained than that for females and 95% of body length and body mass was attained at later ages. Growth in mass lasted a little longer than growth in length for both sexes, following the pattern described for other marine mammals (Chabot & Stenson 2002). Our most pronounced finding, however, was the clearly increased body size of sea otters in the central and western Aleutian archipelago in the 1990s compared with the 1960s/70s. Similar, although more subtle findings were made in Prince William Sound, Alaska following the 1989 Exxon Valdez oil spill. Young female sea otters from an area

where the population remained depressed for several years, and where prey were more abundant, were significantly longer and heavier when compared with a nearby area that remained at high density (Dean *et al.* 2002).

POPULATION STATUS AND BODY CONDITION

The maritime fur trade reduced the western Alaskan sea otter population to near extinction by 1911 (Kenyon 1969). However, after protection, remnant colonies increased rapidly and by the early 1970s had recovered to near maximum levels in some areas (Riedman & Estes 1990). Upon reaching these maximal levels, sea otter habitat across the Aleutians consisted of dense kelp and sparse sea urchin populations (Estes & Duggins 1995), a functional result of high densities of sea otters exerting downward pressure on urchins and relieving grazing pressure. Rapid increases in urchin populations and declines in kelp forests accompanied the recent sea otter decline as top-down pressure on urchins was relieved by reduced sea otter densities (Estes *et al.* 1998, 2004).

It is very clear from the available data that the decline was driven by elevated mortality rate, not reduced fertility or redistribution (Doroff *et al.* 2003; Estes *et al.*

2005). The specific cause of this elevated mortality is, however, somewhat less evident. Available evidence currently supports increased killer whale predation as the most likely cause (Estes *et al.* 1998), a change that Springer *et al.* (2003) attributed to a dietary shift by killer whales toward sea otters following the collapse of sympatric pinniped populations in western Alaska. While the prey-switching component of this hypothesis remains highly speculative, support for the idea that the sea otter decline was caused by killer whales rests in part on (1) direct observations and analyses, and (2) on evidence that is inconsistent with other potential explanations. Estes *et al.* (1998) interpreted the increased abundance of sea urchins during the decline as evidence opposing any sort of nutritional limitation hypothesis for sea otters. The purpose of this study was to evaluate further the evidence for that hypothesis by exploring changes in sea otter body condition.

Our findings suggest that the population declines of sea otters in south-west Alaska are not attributable to nutritional limitation. Changes in the growth functions for both sexes suggest that body condition has improved through time. Sea otters have become significantly heavier and longer with age indicating improved overall health within the population as a whole. Pre-adult growth rates also have increased, further indicating increased resource availability due to reduced conspecific competition. The small numbers of animals measured in 2004 were among the largest and most robust individuals ever examined in the Aleutian Islands, indicating that the trend towards increasing body condition continued into the twenty-first century. These latter findings indicate that the change from resource limited to density-independent growth is a continuous variable with dynamic properties, even at population densities that are far below equilibrium levels.

Length and mass at age provide different views of environmental change. Body length likely reflects conditions experienced in the early years of life, whereas body mass represents recent nutritional status. This is particularly the case with sea otters: extreme examples of a marine mammal that uses income-based as opposed to capital-based maintenance and reproductive strategies (Costa 1988; Bowen, Read, & Estes 2002). Benefits from increased resource availability should be apparent in the body mass of animals of all ages, and this might be expected to vary rapidly in response to a changing environment. The impact of increased resources on body length, however, would be strongest in young animals and should not show any effect after maximum size is attained. This key difference (in the way that resource abundance impacts mass and length) has implications for the use of mass/length ratios as indices of body condition in sea otter populations. Although we did find a trend towards increasing body condition over time (Fig. 6b), the difference was less pronounced for females than males. This likely reflects the increased energetic demands faced by adult females once they reach reproductive age. In addition, there was substan-

tial interannual variance in this index, likely reflecting seasonal and/or year-to-year differences in prey abundance (Monson *et al.* 2000; Watt, Siniff & Estes 2000). This short-term variance may tend to mask longer-term trends in resource abundance, especially if sampling opportunities are limited and time series are less exhaustive than the one available for the present analysis. The solution to this problem may be to analyse age-specific trends in mass and length independently, as we have done here, and to measure alternate indices of resource abundance including direct sampling of prey populations (Dean *et al.* 2002) and time-activity budgets (Gelatt, Siniff & Estes 2002).

POPULATION STRUCTURE

The significant differences in age structure between the 1960s/70s and 1990s (Fig. 8) provide further insight into the demographic changes that accompanied the decline. Assuming no gross biases in age measurement or catchability between shot and live-captured sea otters, the strongly left-skewed age distribution in the 1990s is indicative of almost complete relaxation of age-dependent mortality patterns (i.e. those typical of food-limited populations). Such a scenario is also consistent with the observed changes in body size: juveniles in the 1990s appear to have greatly improved nutritional status, so it is reasonable to expect that their chances of mortality from disease or starvation would be reduced. An increase in pre-weaning and juvenile survival, concurrent with an extremely rapid decrease in population size (Doroff *et al.* 2003), can only be explained by a substantial increase in age-independent mortality, expected under scenarios of human harvest, predation, or some catastrophic event such as an oil spill (Bodkin *et al.* 2000). Of these possible scenarios, predation remains the most plausible hypothesis in light of currently available data (Estes *et al.* 1998).

POTENTIAL SOURCES OF BIAS

It is important to evaluate critically alternative explanations for the patterns evident in our data. Blood or body fluid loss from shot animals would reduce body mass. However, the harvested sea otters were shot in the head to prevent damage to the pelt, resulting in minimal (and if it occurred, consistent) blood and/or fluid loss. Furthermore, animals were weighed and measured nearly directly after death, allowing little time for a reduction in body mass due to loss of fluid. Seasonal fluctuations in body mass potentially biasing results are not relevant in this study because all the samples were obtained during spring and summer (April–August). Thus, the large and significant increases in body mass are mostly likely due to changes in population status and resource availability.

Increases in body length that were seen over the course of this study may be influenced by several factors.

Sea otters relax during sedation, thus length measurements during live captures conducted in the 1990s and 2004 could be biased upwards. Although most of the shot sea otters were measured immediately after death, rigor mortis could have biased length downward. However, the similarities between beach cast carcasses (< 48 h old) and sedated live-captured individuals in California (Fig. 7) suggest minimal post-mortem muscle relaxation or skeletal stretching. Length corrections to the 1960s/70s data set were based on a small sample ($n = 6$) and the majority of the variance in the correction factor was due to variation between individuals. Although length corrections make the relative magnitude of observed differences in L_{∞} somewhat less certain, such corrections do not impact differences in the rate of growth (k) in body length.

Tooth ages based on dental cementum annuli (85% of estimates are shown to be accurate to ± 1 year, Bodkin *et al.* 1997) were available for almost 70% of the individuals. When tooth age was not available, approximate age was estimated based on tooth wear and physical characteristics. There was good correlation between the two types of ages (Fig. 2) and because comparisons were made within a single population utilizing the same prey base (resulting in consistent and comparable tooth wear across individuals), the combination of the two ageing methods was justified after adjustments with the curvilinear model. Note that adjustments to estimated ages with the curvilinear fit in Fig. 2 resulted in the very youngest animals being younger than expected and essentially no age shift until after 8 years of age. Furthermore, no significant differences were found in model parameter estimates using either adjusted or unadjusted estimated ages. Older males and females constituted a smaller proportion of the total sample from the 1990s in our study. However a reasonable sample of animals from this age group was present, so this bias likely did not affect the size-at-age models.

All lines of evidence documented in this study support the general premise that body condition has improved following the precipitous decline of the south-western Alaska sea otter population. There is simply no evidence that the cause of the decline was related to compromised nutritional status. The remaining sea otters in the Aleutian archipelago appear to be thriving. Furthermore, contrasts in age distributions suggest a shift in age structure most consistent with an increase in age-independent survival accompanied by a decrease in age-dependent mortality, indirectly supporting the killer whale predation hypothesis.

The results presented here further support the use of body size as a useful index of changes in ecological conditions experienced by sea otter populations. The causes of population declines in long-lived mammals are notoriously difficult to assess and are often assumed to result from some unspecified aspect of habitat deterioration, especially in the ocean (Pauly *et al.* 2002). Our findings show that retrospective analyses of change in life history characters that vary predictably with population status can be used to distinguish between

general categories of explanations (e.g. density-dependent vs. density-independent factors). We have used body size and age structure, although other metrics can also be informative. The approach taken in this study may provide useful standards for re-evaluating the various explanations proposed for population declines in other species, especially sympatric pinnipeds in the North Pacific for which there is considerable uncertainty and a great deal of present controversy.

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References

- Allee, W.C., Emerson, A.E., Park, O., Park, T. & Schmidt, K.P. (1949) *Principles of Animal Ecology*. Saunders, Philadelphia.
- Ames, J.A., Hardy, R.A., Wendell, F.E. & Geibel, J.J. (1983) *Sea Otter Mortality in California*. Marine Resources Branch, California Fish and Game, Monterey, CA, USA.
- Benz, C.T. & Britton, R.L. (1995) Sea otter capture. *Emergency Care and Rehabilitation of Oiled Sea Otters* (eds T.M. Williams & R.W. Davis), pp. 23–38. University of Alaska, Fairbanks, Alaska.
- Berryman, A.A. (2004) Limiting factors and population regulation. *Okios*, **105**, 667–670.
- von Bertalanffy, L. (1938) A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology*, **10**, 181–213.
- Bodkin, J.L., Ames, J.A., Jameson, R.J., Johnson, A.M. & Matson, G.M. (1997) Accuracy and precision in estimating age of sea otters using cementum layers in the first premolar. *Journal of Wildlife Management*, **61**(3), 967–973.
- Bodkin, J.L., Burdin, A.M. & Ryazanov, D.A. (2000) Age- and sex-specific mortality and population structure in sea otters. *Marine Mammal Science*, **16**, 201–219.
- Bowen, W.D., Read, A.J. & Estes, J.A. (2002) Feeding ecology. *Marine Mammal Biology: an Evolutionary Approach* (ed. A.R. Hoelzel), pp. 217–246. Blackwell Publishing, Oxford.
- Bowen, W.D., Ellis, S.L., Iverson, S.J. & Boness, D.J. (2003) Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals, *Phoca vitulina*, on Sable Island. *Journal of Zoology, London*, **261**, 155–163.
- Boyd, I.L. (1984) The relationship between body condition and the timing of implantation in pregnant gray seals. *Journal of Zoology, London*, **203**, 113–123.

- Calkins, D.G., Becker, E.F. & Pitcher, K.W. (1998) Reduced body size of female steller sea lions from a declining population in the Gulf of Alaska. *Marine Mammal Science*, **14**, 232–244.
- Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*, 2nd edn. Sinauer Associates, Sunderland, MA.
- Chabot, D. & Stenson, G.B. (2002) Growth and seasonal fluctuations in size and condition of male Northwest Atlantic harp seals *Phoca groenlandica*: an analysis using sequential growth curves. *Marine Ecology Progress Series*, **227**, 25–42.
- Costa, D.P. (1988) Methods for studying the energetics of freely diving animals. *Canadian Journal of Zoology*, **66**, 45–52.
- Costa, D.P. & Kooyman, G.L. (1982) Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. *Canadian Journal of Zoology*, **60**, 2761–2767.
- Costa, D.P., Croxall, J.P. & Duck, C.D. (1989) Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology*, **70**, 596–606.
- Dean, T.A., Bodkin, J.L., Fukuyama, A.K., Jewett, S.C., Monson, D.H., O'Clair, C.E. & VanBlaricom, G.R. (2002) Food limitation and the recovery of sea otters following the 'Exxon Valdez' oil spill. *Marine Ecology Progress Series*, **241**, 255–270.
- Doak, D.F. & Morris, W. (1999) Detecting population-level consequences of ongoing environmental change without long-term monitoring. *Ecology*, **80**, 1537–1551.
- Doroff, A.M., Estes, J.A., Tinker, M.T., Burn, D.M. & Evans, T.J. (2003) Sea otter population declines in the Aleutian archipelago. *Journal of Mammalogy*, **84**, 55–64.
- Eberhardt, L.L. (1988) Using age structure data from changing populations. *Journal of Applied Ecology*, **25**, 373–378.
- Estes, J.A. (1989) Adaptations for aquatic living in carnivores. *Carnivore Behavior Ecology and Evolution* (ed. J.L. Gittleman), pp. 242–282. Cornell University Press, Ithaca, NY.
- Estes, J.A. (1990) Growth and equilibrium in sea otter populations. *Journal of Animal Ecology*, **59**, 385–400.
- Estes, J.A. & Duggins, D.O. (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs*, **65**, 75–100.
- Estes, J.A. & VanBlaricom, G.R. (1985) Sea otters and shellfisheries. *Marine Mammals and Fisheries* (eds J.R. Beddington, R.J.H. Beverton & D.M. Lavigne), pp. 187–235. George Allen & Unwin, London.
- Estes, J.A., Jameson, R.J. & Rhode, E.B. (1982) Activity and prey selection in the sea otter: Influence of population status on community structure. *American Naturalist*, **120**, 242–258.
- Estes, J.A., Tinker, M.T., Williams, T.M. & Doak, D.F. (1998) Killer whale predation on sea otters linking coastal with oceanic ecosystems. *Science*, **282**, 473–476.
- Estes, J.A., Danner, E.M., Doak, D.F., Konar, B., Springer, A.M., Steinberg, P.D., Tinker, M.T. & Williams, T.M. (2004) Complex trophic interactions in kelp forest ecosystems. *Bulletin of Marine Sciences*, **74**, 621–638.
- Estes, J.A., Tinker, M.T., Doroff, A.M. & Burn, D.M. (2005) Continuing sea otter population declines in the central and western Aleutian archipelago. *Marine Mammal Science*, **21**, 169–172.
- Fowler, C.W. & Siniff, D.B. (1992) Determining population status and the use of biological indices in the management of marine mammals. *Wildlife 2001: Population* (eds D.R. McCullough & R.H. Barrett), pp. 102–103. Elsevier Applied Science, London.
- Gelatt, T.S., Siniff, D.B. & Estes, J.A. (2002) Activity patterns and time budgets of the declining sea otter population at Amchitka Island, Alaska. *Journal of Wildlife Management*, **66**, 29–39.
- Gerber, L.R., Tinker, T.M., Doak, D. & Estes, J.A. (2004) Mortality sensitivity in life-stage simulation analysis: a case study of southern sea otters. *Ecological Applications*, **14**, 1554–1565.
- Green, A.J. (2001) Mass/length residuals: Measures of body condition or generators of spurious results? *Ecology*, **82**, 1473–1483.
- Guniet, C., Roux, J.P., Bonnet, M. & Milson, V. (1998) Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. *Canadian Journal of Zoology*, **76**, 1418–1424.
- Kappenman, F.K. (1981) A method for growth curve comparisons. *Fishery Bulletin*, **79**, 95–101.
- Kenyon, K.W. (1969) The sea otter in the eastern Pacific Ocean. *North American Fauna*, **68**, 1–352.
- Lunn, N.J. & Boyd, I.L. (1993) Effects of maternal age and condition on parturition and the prenatal period of Antarctic fur seals. *Journal of Zoology*, **229**, 55–67.
- McMahon, C.R., Burton, H.R. & Bester, M.N. (2000) Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science*, **12**, 149–153.
- Monson, D.H. & Degange, A.R. (1995) Reproduction, preweaning survival, and survival of adult sea otters at Kodiak Island, Alaska. *Canadian Journal of Zoology*, **73**, 1161–1169.
- Monson, D., Estes, J.A., Siniff, D.B. & Bodkin, J.B. (2000) Life history plasticity and population regulation in sea otters. *Oikos*, **90**, 457–468.
- Monson, D.H., McCormik, C. & Ballachey, B.E. (2001) Chemical anesthesia of northern sea otters (*Enhydra lutris*): results from past field studies. *Journal of Zoology and Wildlife Medicine*, **32**, 181–189.
- Pauly, D., Christensen, V., Guenette, S., Pitcher, T.J., Sumalia, U.R., Walters, C.J., Watson, R. & Zeller, D. (2002) Towards sustainability in world fisheries. *Nature*, **418**, 689–695.
- Ricker, W.E. (1979) Growth rates and models. *Fish Physiology: Bioenergetics and Growth* (eds W.S. Hoar, D.J. Randall & J.F. Brett), pp. 667–743. Academic Press Inc., Orlando, FL.
- Riedman, M.L. & Estes, J.A. (1990) The sea otter (*Enhydra lutris*): behavior, ecology, and natural history. *US Department of the Interior, Fish and Wildlife Service Biological Report*, **90**(14), 126pp.
- Silva, M. (1998) Allometric scaling of body length: elastic or geometric similarity in mammalian design. *Journal of Mammalogy*, **79**, 20–32.
- Soto, K.H., Trites, A.W. & Arias-Schreiber, M. (2004) The effects of prey availability on pup mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru. *Journal of Zoology London*, **264**, 419–428.
- Springer, A.M., Estes, J.A., Van Vliet, G.B., Williams, T.M., Doak, D.F., Danner, E.M., Forney, K.A. & Pfister, B. (2003) Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences USA*, **100**(21), 12223–12228.
- Stewart, R.E.A. (1994) Size-at-age relationships as discriminators of white whale (*Delphinapterus leucas*) stocks in the eastern Canadian Arctic. *Meddelelser Om Grønland, Bioscience*, **39**, 217–225.
- Trites, A.W. & Bigg, M.A. (1992) Changes in body growth of northern fur seals from 1958 to 1974: density effects of changes in the ecosystem? *Fisheries Oceanography*, **1**(2), 127–136.
- Udevitz, M.S. & Ballachey, B.E. (1998) Estimating survival rates with age-structure data. *Journal of Wildlife Management*, **62**, 779–792.
- Watt, J., Siniff, D.B. & Estes, J.A. (2000) Inter-decadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska. *Oecologia (Berlin)*, **124**, 289–298.
- Winship, A.J., Trites, A.W. & Calkins, D.G. (2001) Growth in body size of the Steller sea lion (*Eumetopias jubatus*). *Journal of Mammalogy*, **82**(2), 500–519.

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