OCS Study
MMS 2006-007

Population Dynamics and Biology of the California Sea Otter (*Enhydra lutris nereis*) at the Southern End of its Range

Final Technical Summary

Final Study Report

U.S. Department of the Interior
Minerals Management Service
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FINAL TECHNICAL SUMMARY

STUDY TITLE: Population Dynamics and Biology of the California Sea Otter (*Enhydra lutris nereis*) at the Southern End of its Range

REPORT TITLE: Population Dynamics and Biology of the California Sea Otter (*Enhydra lutris nereis*) at the Southern End of its Range

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KEY WORDS: sea otter, mark-recapture, radio telemetry, demography, spatially structured model, foraging behavior, dietary specializations, dive depths, activity budgets, thermoregulation, energetic costs, health parameters, disease ecology.

BACKGROUND: Sea otters (*Enhydra lutris*) were hunted to near extinction during the Pacific maritime fur trade. Further hunting was prohibited by international treaty in 1911, at which time a dozen or so remnant colonies survived. The southern sea otter (*E. l. nereis*) is descended from one of these remnant colonies that survived along the Big Sur coastline of central California and

contained perhaps as few as 50 individuals at the beginning of the 20th century. While sea otter populations elsewhere in the North Pacific Ocean recovered at rates of 17-20% yr-1, the California population has never grown at more than one-third this rate and is currently listed as Threatened under the Endangered Species Act. Concerns over oil and gas development were the principal reasons for listing, and the criteria for changing the population's official status by de-listing or up-listing it (to Endangered) are based on oil spill risk analysis.

Except for a period of decline from the mid 1970s to early 1980s that is now thought to have resulted from entanglement mortality, the California sea otter population continued increasing at a slow rate, approximately 5% per year, until the mid-1990s. About 1995, however, the population dynamics changed for unknown reasons and the population began to decline, with annual population counts steadily decreasing through 1999. Even though the population was declining, the geographic range of the population was continuing to expand both to the north and south. A better understanding of the changes in natural history and population dynamics underlying these phenomena was of interest to several federal and state agencies, including the US Fish and Wildlife Service (USFWS), the Minerals Management Service (MMS), and The Department of Fish and Game (DFG).

Range expansion to the south was of particular interest because it brought sea otters into closer association with the potential effects of oil and gas development. This expansion was characterized by a seasonal redistribution of up to several hundred individuals from northern areas to the southernmost part of the range. Most of these otters congregated 5-40 km southeast of Point Conception during the winter and spring. Thought to be mostly non-territorial males, these individuals were believed to rejoin the more northern population during the summer and autumn, but exactly where they went was unknown. Because these individuals traveled seasonally, and because both range expansion and population decline could conceivably be due to a single causal factor such as depletion of food resources to the north, we argued that it was not possible to understand the population dynamics of these otters in the most southern part of the range without a better understanding of the population as a whole.

OBJECTIVES: The present study was designed to obtain an updated picture of population dynamics and movement patterns, as well as an increased understanding of the problems currently facing the population. We had three main objectives: 1) to better understand how overall population dynamics had changed since the mid-1980s (a period for which data exist from a previous MMS-funded study) and the reasons for the recent population decline; 2) to describe the population dynamics, behavior and seasonal movement patterns of sea otters at the southern end of their range; and 3) to examine the inter-relationships between nutritional requirements, foraging strategies, energetics, and activity patterns and the ways in which these relationships determine habitat suitability for sea otters in California.

DESCRIPTION: In pursuit of these objectives, we undertook extensive field, captive and laboratory studies. Range-wide surveys of the entire population and analyses of beach-cast carcasses were continued using established protocols. Population surveys were conducted in spring and fall using standardized techniques developed by federal and state biologists and in use since 1982. Carcass data were obtained, stored and analyzed based on standardized procedures in place since the early 1990s. The freshest carcasses were necropsied by trained veterinary pathologists. Information from these two long-term databases was used in the development of spatially-structure population models.

Radio-telemetry methods were used to study two groups of instrumented otters: the first group contained 47 individuals (35 females and 12 males) captured in the center of the range just south of Pt. Piedras Blancas, and near the towns of Cambria and San Simeon. The second group contained 25 individuals (24 males and one female) captured south of Point Conception. All study animals were instrumented with surgically implanted VHF radio transmitters. Thirty-three animals (30 at Piedras Blancas, 3 at Point Conception) were also equipped with archival time-depth recorders (TDR's). Radios were equipped with thermal monitors that allowed us to record body temperature whenever we were in contact with an individual. The radios allowed us to track individuals, while the TDR's simultaneously stored a continuous time record of dive profiles.

Data collected from intensive monitoring of these instrumented animals contributed to estimates of current survival and reproductive rates and analyses of movement patterns, foraging ecology, activity patterns and diving behavior, and temperature dynamics. Experiments with captive otters at Long Marine Laboratory, University of California Santa Cruz, provided supplementary information on the energetic costs of diving. Data from the TDR's allowed for more in-depth analyses of activity patterns and diving behavior.

SIGNIFICANT CONCLUSIONS: The tagging studies confirm that adult sea otters have strong affinities to particular locales and that these affinities are usually maintained throughout their lives, even though individual otters sometimes move long distances. Strong patterns of dietary specialization by both males and females may act to limit individuals to particular habitat types or locations. Adult females in particular, due to the extreme energetic demands of reproduction and lactation, may be restricted to their home ranges by the need to maintain high rates of energy input, accomplished by a high degree of specialization on a few prey types. Prey specialization is associated with differences in diving behavior between animals utilizing alternative diet types. Three distinct feeding strategies were identified, and these are likely maintained by a combination of frequency/density dependence and correlational selection.

In contrast to limited female movements, our results indicated that male animals found south of Pt. Conception are particularly likely to move throughout the existing sea otter range in California (i.e. from Santa Barbara north to Half Moon Bay). The corollary to this pattern is that many adult and sub-adult males throughout the range tend to move to the southern range periphery during the late winter and early spring (although such movements may also occur at other times of year). The precise reasons for these movements are still uncertain, although we now have considerable evidence to suggest that access to increased food availability at the southern range periphery is a likely motivation, and is certainly a beneficial nutritional consequence. Whatever the proximate reasons for these movements, we see the benefits reflected in improved body condition, reduced foraging behavior, and increased survival. These movements also provide a means of internal connectivity to the entire California sea otter population--the potential for gene flow, disease transfer, and any other feature that might be carried by an individual through a population as it moves through space and time.

Our findings also revealed a larger scale pattern of spatial structure in the California sea otter population – a significant difference in behavior and demography between animals that live at the northern and southern ends of the range. Sea otters at the southern end of their range appear to be less limited by resource availability than they are in the north or range center. Sea otters in the center of the range spend more time feeding than animals south of Pt. Conception, or as compared to sea otters in the 1980's. Overall survival rates also are somewhat higher in the south than they are in the north and center of the range, and movement patterns differ significantly between these two regions. Female survival has decreased since the 1980's, particularly for prime-age adults,

but reproductive rates have not changed and male survival has remained constant or even increased. This spatial pattern of variation in survival will have important consequences for future population growth and range expansion to the south: we develop a mathematical model with which to predict future dynamics and evaluate the sensitivity of these predictions to age/sex/location-specific vital rates and movement probabilities. This model indicates that movement and dispersal patterns of sub-adult females at the south end of the range will have the greatest effect on southward range expansion, but the survival of females in the center of the range will have a greater impact on the growth of the population as a whole.

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FINAL STUDY REPORT

Chapter 1. Introduction and overview of methods

Katherine Ralls, M. Tim Tinker, and James A. Estes

Sea otters (*Enhydra lutris*) were hunted to near extinction during the Pacific maritime fur trade (Kenyon 1969). Further hunting was prohibited by international treaty in 1911, at which time a dozen or so remnant colonies survived. The California (or southern) sea otter (*E. l. nereis*) is descended from one of these remnant colonies that survived along the Big Sur coastline of central California and contained perhaps as few as 50 individuals at the beginning of the 20th century (Riedman and Estes 1990). While sea otter populations elsewhere in the North Pacific Ocean recovered at rates of 17-20% yr^{-1}, the California population has never grown at more than one-third this rate (Estes 1990) and is currently listed as Threatened under the Endangered Species Act. Concerns over oil and gas development were the principal reason for listing, and the criteria for changing the population's official status by de-listing or up-listing it (to Endangered) are based on oil spill risk analysis (USFWS 2003).

Except for a period of decline from the mid 1970s to early 1980s that is now thought to have resulted from entanglement mortality, the California sea otter population continued increasing at a slow rate, approximately 5% per year, until the mid-1990s. About 1995, however, the population dynamics changed for unknown reasons and the population began to decline, with annual population counts steadily decreasing through 1999 (USFWS 2003). Even though the population was declining in abundance, the geographic range of the population was continuing to expand both to the north and south. A better understanding of the changes in natural history and population dynamics underlying these phenomena was of interest to several federal and state agencies, including the US Fish and Wildlife Service (USFWS), the Minerals Management Service (MMS), and The Department of Fish and Game (DFG).

Range expansion to the south was of particular interest to MMS because it brought sea otters into closer association with the potential effects of oil and gas development. This expansion was characterized by a seasonal redistribution of up to several hundred individuals from northern areas to the southernmost part of the range. Most of these otters congregated 5-40 km southeast of Point Conception during the winter and spring (Figure 1). Thought to be largely non-territorial males, these individuals were believed to rejoin the more northern population during the summer and autumn, but exactly where they went was unknown. Because these individuals traveled seasonally, and because both range expansion and population decline could conceivably be due to a single causal factor such as depletion of food resources to the north, we argued that it was not possible to understand the population dynamics of these otters in the most southern part of the range without a better understanding of the population as a whole.

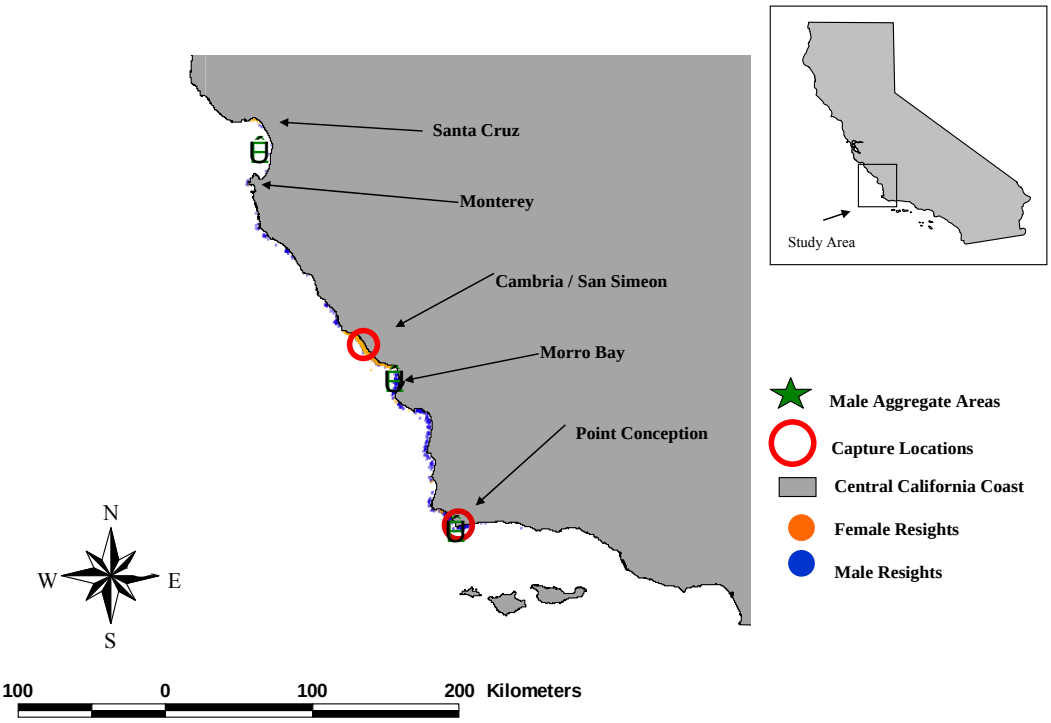

Figure 1. Map of central California showing two primary study areas and re-sighting locations of radio-tagged study animals between 2001 and 2004.

In 2001, when we began the work described in this report, our knowledge of the dynamics of the southern sea otter population was largely based on a previous MMS-funded study (Siniff and Ralls, 1988) conducted during the 1980s when the population was increasing. The present study was designed to obtain an updated picture of population dynamics and movement patterns as well as an increased understanding of the problems currently facing the population. We had three main objectives: 1) to better understand how overall population dynamics had changed since the mid-1980s and the reasons for the population decline; 2) to describe the population dynamics, behavior and seasonal movement patterns of sea otters at the southern end of their range; and 3) to examine the inter-relationships between nutritional requirements, foraging strategies, energetics, and activity patterns and the ways in which these relationships determine habitat suitability for sea otters in California.

In pursuit of these objectives, we undertook extensive field, captive and laboratory studies. Range-wide surveys of the entire population and analyses of beach-cast carcasses were continued using established protocols. Population surveys were conducted in spring and fall using standardized techniques developed by federal and state biologists and in use since 1982 (Estes and Jameson 1988). Carcass data were obtained, stored and analyzed based on standardized procedures in place since the early 1990s (Estes et al. 2003). The freshest carcasses were necropsied by trained veterinary pathologists. Information from these two long-term databases was used in the development of the new population models described in Chapter 2.

New field efforts focused on two groups of instrumented otters (Appendix D). The first group contained 47 individuals (35 females and 12 males) captured in the center of the range just south of Pt. Piedras Blancas, and near the towns of Cambria and San Simeon (Figure 1). The second group contained 25 individuals (24 males and one female) captured south of Point Conception. All study animals were instrumented with surgically implanted VHF radio transmitters (Ralls et al. 1989). Thirty three animals (30 at Piedras Blancas, 3 at Point Conception) were also equipped with archival time-depth recorders (TDRs). Radios were equipped with thermal monitors that allowed us to record body temperature whenever we were in contact with an individual. The radios allowed us to track individuals, while the TDRs simultaneously stored a continuous time record of dive profiles. Data collected from intensive monitoring of these instrumented animals contributed to our estimates of current survival and reproductive rates (Chapter 2) and analyses of movement patterns (Chapter 3), foraging ecology (Chapter 5), activity patterns and diving behavior (Chapter 6), and temperature dynamics (Chapter 7). Experiments with captive otters at Long Marine Laboratory, University of California Santa Cruz, provided supplementary information on the energetic costs of diving (Chapter 7). Data from the TDRs made a major contribution to Chapter 6 (activity patterns and diving behavior).

A third group of sea otters was captured and instrumented in the Monterey Bay area for a study led by James L. Bodkin, US Geological Survey, and Michelle Staedler, Monterey Bay Aquarium. These investigators kindly contributed data from their study to Chapters 2 (demography) and 5 (foraging ecology). Data on all three groups of instrumented animals were collected so as to be compatible with data collected in the earlier study of radio-tagged otters in California (Siniff and Ralls 1988). This comparable approach to data collection helped us to determine which aspects of sea otter demography, behavior, and ecology had changed since the 1980s.

A series of standardized morphometric data (weight, length, tooth wear and body condition) as well as various samples (blood, swabs for bacterial culture) were obtained from each captured otter. This information, as well as necropsy data from the instrumented animals that died during the study, provided the basis for the information on animal health presented in Chapters 9 and 10.

By using the multifaceted and highly collaborative approach described above, which involved contributions from numerous researchers with a variety of technical backgrounds, we were able to achieve the greatly increased understanding of the California sea otter population described in this report.

Chapter 2. Spatial and temporal variation in sea otter demography

M. Tim Tinker, Daniel F. Doak, James A. Estes, Brian B. Hatfield, Michelle M. Steadler and James L. Bodkin

Abstract

1) Better information on historical and current population dynamics is central to understanding patterns of growth and decline in the California sea otter population. We developed a maximum likelihood-based analytical method to estimate historical age/sex specific vital rates as well as spatial and temporal variation in vital rates from longitudinal databases on population census numbers and the age-structure of salvaged carcasses.

2) We estimated current demographic parameters by conducting a mark-recapture study, measuring survival and reproduction of 115 radio-tagged individuals between 2001 and 2004. These current estimates were compared to estimates from a similar study of radio-tagged otters conducted in the mid-eighties.

3) Together, these two approaches indicated that survival has decreased substantially between the early 1990s and the present and is lowest in the north-central portion of the population's range.

4) The greatest decrease in survival was for adult females (≥ 4 years of age). Variation in the survival of this age/sex class is primarily responsible for regulating population growth and driving population trends.

Introduction

Spatial and temporal variation in population abundance is a universal characteristic of all wildlife species, and understanding the causes of such variation is a fundamental goal of population biologists (Caughley 1977). Unfortunately, while it is often straightforward to detect trends in population abundance, determining the cause of observed trends is generally much more difficult. Populations vary in abundance due to changes in the vital rates of individual animals (birth, death, immigration and emigration), which are shaped by an almost infinite array of biotic and abiotic factors. Nonetheless, determining the patterns and sources of variation in demographic rates is a necessary step in the assessment of population viability (Doak and Morris 2002), and analytical models that incorporate demographic variation have been important tools in the conservation of threatened populations such as the Yellowstone grizzly bear (Eberhardt et al. 1994, Doak 1995, Pease and Mattson 1999) and the northern spotted owl (Lande 1991, Forsman 1993).

Unfortunately, for many endangered or threatened species there are few (or no) reliable estimates of demographic rates. Direct estimates are difficult and costly to acquire, requiring longitudinal records from marked individuals: such records are generally obtained using tagging, band recovery or biotelemetry methods, collectively referred to as "mark-recapture" data (White 1983, Pollock et al. 1990). In the case of large vertebrate species with broad geographic ranges and long life spans it is particularly difficult to obtain mark-recapture data over long enough time periods and over sufficiently large areas to form a representative picture of the key demographic drivers of population dynamics. In the few cases where demographic data have been collected over appropriate spatial and temporal scales for large vertebrates, the resulting data sets have provided powerful tools for projecting future population dynamics and/or identifying key life history stages for focusing management efforts (e.g. Crouse et al. 1987, Eberhardt et al. 1994, Crooks et al. 1998, Coulson et al. 1999, Milner-Gulland et al. 2000, Schaefer et al. 2001). However, for most large species it is either unfeasible to initiate large scale mark-recapture programs, or else mark-recapture programs were not in place when important population dynamics were occurring. For example, in the case of the California sea otter (*Enhydra lutris nereis*) a mark-recapture program now underway provides estimates of recent demography (this paper), but cannot shed light on past population declines.

Given the above-mentioned limitations of mark-recapture studies, it is clearly important to develop alternative methods for inferring demography of populations, making most effective use of whatever data sets are available (Doak and Mills 1994). One alternative method is the indirect estimation of demographic rates from population age structure (Caughley 1977). Although the reliability of indirect estimates based on standing age structure has traditionally been restricted by the assumption of constant population size, methodological variations have been proposed that circumvent this assumption (e.g. Eberhardt 1988, Udevitz and Ballachey 1998, Doak and Morris 1999). Unfortunately, for many non-harvested species there is no reliable means of measuring the standing age structure, particularly if lethal or invasive sampling is not feasible (i.e. for many endangered species) and there are no visually obvious individual features that correlate with age. One way around this problem is to sample dead animals rather than live ones: a method proposed by Doak and Morris (1999) provides a means of inferring demographic rates, and variation in those rates, using the age

structure of death assemblages. For many vertebrate species, carcasses can be collected with little effort and age estimates derived by sectioning of bones or teeth (Matson 1981, Bodkin et al. 1997): for example, this method was recently used to assess the long-term impact of a major environmental perturbation (the Exxon Valdez oil spill) on a population of sea otters in Prince William Sound by measuring changes in the age-structure of beach-cast carcasses (Monson et al. 2000a). In addition to indirect estimates based on age-structure, simple population counts conducted over many years may be useful for evaluating alternative hypotheses about variation in demographic rates (Hilborn and Mangel 1997, Doak and Morris 2002), particularly if these counts are structured by developmental stage (e.g. juveniles vs. adults, Pascual and Adkison 1994).

Here we develop a methodological approach to inferring patterns of demographic variation in a population. In part 1, we extend the methodology described by Monson *et al.* (2000a) to include an assessment of spatial as well as temporal variation in demography, to incorporate other data sources besides carcass age structure (in particular, population counts), and to more formally incorporate model uncertainty. Next, in part 2, we apply this method to the California (or southern) sea otter, a protected sub-species with "Threatened" status under the Endangered Species Act (USFWS 2003). Although range-wide counts indicate unequivocally that population recovery ceased in the mid 1990's (Figure 2), it is less clear what specific demographic changes were responsible for the change in population dynamics.

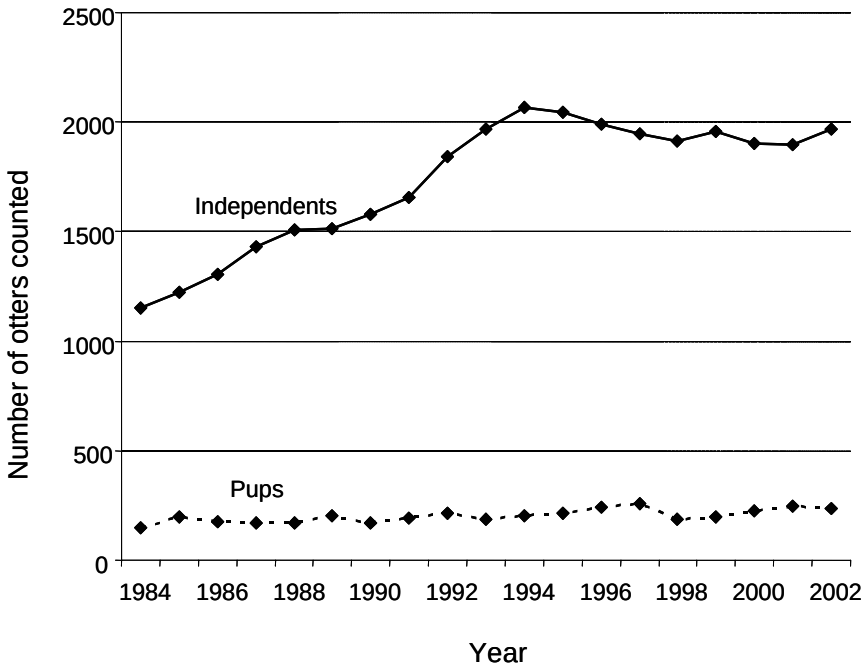

Figure 2. Annual range-wide counts of southern sea otters, *Enhydra lutris nereis*, conducted between 1984 and 2002. Values represent the three-year running average of the spring counts of independents (solid line) and the annual average of the spring and fall counts of dependent pups (dashed line).

Data presented by Estes *et al.* (2003) indicate that periods of decline in southern sea otters are associated with increased mortality rather than decreased birth rates: we now investigate in greater detail the spatial and temporal changes in demographic processes that halted population recovery in the 1990s. Reliable demographic information is needed to guide decision making on management options currently under consideration (Greg Sanders, US Fish & Wildlife Service, pers. comm.) and to ensure the long-term recovery of this population (USFWS 2003). The analytical approach described here provides such information, and at the same time raises important questions about the way that model selection methods can be used in the context of complex models and data sets, as we discuss.

Methods

Part 1: Estimating past demographic rates (1992-2001)

Field data

Two types of field data were available for the period of interest: population counts and beach-cast carcasses classified by age, sex and location of recovery. Standardized, range-wide population counts of the southern sea otter are conducted twice annually (Estes and Jameson 1988, Estes *et al.* 2003): a spring survey (early May) provides the primary index of population growth for this population, while a fall survey (early November) is conducted primarily to better estimate the pup production data. On road-accessible stretches of coastline (~45% of the current range), counts are conducted by experienced teams of shore-based observers using binoculars and spotting scopes. The remaining areas (~55% of the current range) are counted from fixed-wing aircraft: three observers and a pilot conduct the aerial counts by flying transects parallel to shore and spaced approximately 800 m apart, at an air speed of 90 nm/hr, and at 65 m elevation. The aerial portions include many low-density areas, so that the proportion of animals counted from the aircraft is generally about 20% of the total count. For both ground and aerial counts, each otter (or group of otters) is marked onto a 1:20,000 coastline map, and these maps are later digitized into a GIS database. The net result of the survey is an uncorrected, minimum count of independent otters and dependent pups (0 – 6 months of age). For independent otters we used 11 spring counts made during the period 1992–2002: the numbers counted during these surveys ranged from 1790 to 2095. For dependent pups we used the average of the spring and fall counts made during the same period: using the mean number from these two surveys reduced the effect of any seasonal variation in the number of dependent pups present during a given census.

The California Department of Fish and Game (CDF&G) and the Biological Resources Division of the U.S. Geological Survey (USGS) have maintained a salvage network to collect beach-cast carcasses of sea otters since 1968. Information about beach-cast carcasses – date of recovery, sex, age-class, length, weight, condition, recovery location, and cause of death – is added to a database maintained by U.S. Geological Survey (Pattison et al. 1997). Estes *et al.* (2003) provided a recent summary of this database, which currently contains data from over 3900 carcasses. Since 1992, tooth-age estimates have been collected from all beach-cast carcasses, with the exception of pups (<100 cm total length) and those

for which an unbroken premolar could not be obtained. Age-at-death was estimated by cementum analysis of a single upper premolar tooth (Bodkin et al. 1997) using consistent methods (Matson's Laboratory, Milltown MT), and each age estimate was accompanied by a quality code of A (excellent), B (good) or C (poor). For the current analysis, we used ages from all carcasses collected between January 1992 and December 2001, with estimated age of 1 or more and quality code of A or B, for a total sample size of 742. We excluded 0-year old carcasses because they were underrepresented in the carcass record to an unknown degree, mainly as a result of increased susceptibility of small carcasses to decomposition or scavenging (Ames et al. 1983, Pattison et al. 1997, Estes et al. 2003).

Overview of Modeling Approach

Our general approach can be broken into five steps: 1) use logit functions to predict population vital rates (survival and reproduction) that vary by age, sex, time period and geographic area; 2) use these estimated rates to construct a modified Leslie matrix for the population, and use this matrix to project population growth (and track age structure) over the study period. This results in expected population counts for each year, as well as expected age-distributions of individuals dying each year; 3) compare the expected population counts and carcass age structures with the field data, and use maximum likelihood techniques to find the parameter values that best predict the observed data; 4) repeat steps 1–3 using many different logit functions to predict vital rates, varying in complexity (and thus number of parameters) and allowing for different combinations of main effects (age, sex, time and location) and interactions; 5) use information theory (AIC methods) to select the set of "best" models (those model forms that provide most predictive power and maximum parsimony), and use this set of models to describe underlying demographic changes over the study period, while accounting for model uncertainty. We explain each of these steps in the following sections.

Formulating age-, sex-, time- and location-dependent demographic rates

Although sea otter births can occur throughout the year (Wendell et al. 1984, Jameson and Johnson 1993), we formulated our model in terms of discreet age classes, with the time-step set to 1 year. This simplifies presentation of results, and better corresponds to the discreet age scores resulting from the tooth cementum analysis. A discrete model was also appropriate because a) total population counts were made annually, and thus expected vs. observed population growth could only be evaluated in yearly intervals; and b) reproduction in mature sea otters, although occurring throughout the year, is effectively an annual event at the level of the individual: gestation lasts approximately 6 months, followed by the birth of a single offspring that is dependant on exclusive maternal care for a period of approximately 6 months, resulting in a maximum reproductive output of 1 weaned offspring per female, per year (Wendell et al. 1984, Jameson and Johnson 1993). The vital rates of concern are annual survival probabilities (s) and, for females, annual birth rates (b) and weaning success rates (w). We assumed that vital rates might vary as a function of age, sex, time period and location.

The probability that a single sea otter (age x, sex y, located within geographic area g) would survive from year t to year t+1 was estimated using a logit function of the form:

$$s_{x,y,t,g} = \frac{e^{f_x+f_y+f_t+f_g}}{1+e^{f_x+f_y+f_t+f_g}} \qquad \mathbf{1}$$

where f_x, f_y, f_t, and f_g are sub-functions that specify the effects of age, sex, time and location, respectively. We conducted all calculations for animals aged 1 year or greater (x = 1, 2… 19 years old): for the first year class, x = 0, we set survival probabilities equal to that of 1 year olds (x = 1). While this is likely a reasonable approximation (Monson et al. 2000a), we have no way to directly gauge its validity because we could not include 0-year old carcasses in the maximum likelihood fitting, due to potential bias (see above).

The first sub-function, f_x, accounted for variation due to year class:

$$f_x = x \cdot \theta_1 + x^2 \cdot \theta_2 + x^3 \cdot \theta_3 + \frac{1}{x}\left(\frac{\theta_4}{1-\theta_4}\right) \qquad \mathbf{2}$$

where [θ_1 θ_2 θ_3 θ_4] is an array of fitted parameters (for all equations, θ symbols indicate fitted parameters). Equation 2 is essentially a linear, 3rd-order polynomial function with an additional term added to allow for greater flexibility in fitting juvenile survival. When converted to a logit, this function generally results in an "inverted U" shaped survival curve, typical of large mammals (Caughley 1977), but is sufficiently flexible to fit a wide range of survivorship schedules. Two previous demographic models constructed for sea otters (Eberhardt and Siniff 1988, Siniff and Ralls 1988) have used a competing-risks function to model survivorship (Siler 1979, Eberhardt 1985), a slightly different approach to that employed here. The chief advantage of the competing-risks function (also called a proportional hazards function) is that the fitted parameters can be interpreted directly as age-specific mortality risks. The advantages of the logit function (equation 1) are that fewer parameters are required to account for the effect of age (4 *vs*. 5 parameters) and the function can be easily expanded to include other effects (e.g. sex, time and location). For our purposes the important question is whether one function provides a better fit to empirical data. Using age-specific survival estimates for southern sea otters in the 1980s as a sample data set (Siniff and Ralls 1988), we compared the goodness-of-fit of a 4-parameter logit function (i.e. equation 1 and 2) with that of a 5-parameter, competing-risks model (Eberhardt 1985). The logit function resulted in a fitted curve virtually identical to that produced by the competing-risks function, and provided equivalent goodness of fit (adjusted R^2 = 0.995 for both functions).

We incorporated male-female differences in survival using the function:

$$f_y = y \cdot \theta_5 + x \cdot y \cdot \theta_6 \qquad \mathbf{3}$$

where y = 0 for females and y = 1 for males. Equation 3 allows for lower or higher survival of males relative to females, as well as a simple age-sex interaction.

To allow for temporal variation in survival, we used one of two functions: f_t^1 was used to model smoothly changing survival rates, while f_t^2 was used to model discrete time effects. In the first scenario, we modeled changes in survival that could be gradual or rapid, but were still continuous across years:

$$f_t^1 = t \cdot \theta_7 + t^2 \cdot \theta_8 + t^3 \cdot \theta_9 + t \cdot x \cdot \theta_{10} + t \cdot y \cdot \theta_{11} + t \cdot x \cdot y \cdot \theta_{12} \qquad \textbf{4}$$

Equation 4 allows for both linear and higher order time effects, as well as interactions between time, age and sex. As an alternative to a continuous time effect, we also considered changes in survival that may have occurred suddenly, effectively treating time as a categorical variable:

$$f_t^2 = A \cdot \theta_{13} + A \cdot x \cdot \theta_{14} + A \cdot y \cdot \theta_{15} + A \cdot x \cdot y \cdot \theta_{16} \qquad \textbf{5}$$

where A is a switch variable: $A = 0$ if $t < \theta_t$, $A = 1$ if $t \geq \theta_t$, and θ_t is a fitted parameter that specifies the temporal breakpoint in survival probabilities. As with equation 4, equation 5 allows for interactions between time, age and sex. As shown, equation 5 allows for two time categories; however, by adding additional switch variables (and thus additional fitted parameters), we also fit models allowing for three or four time categories.

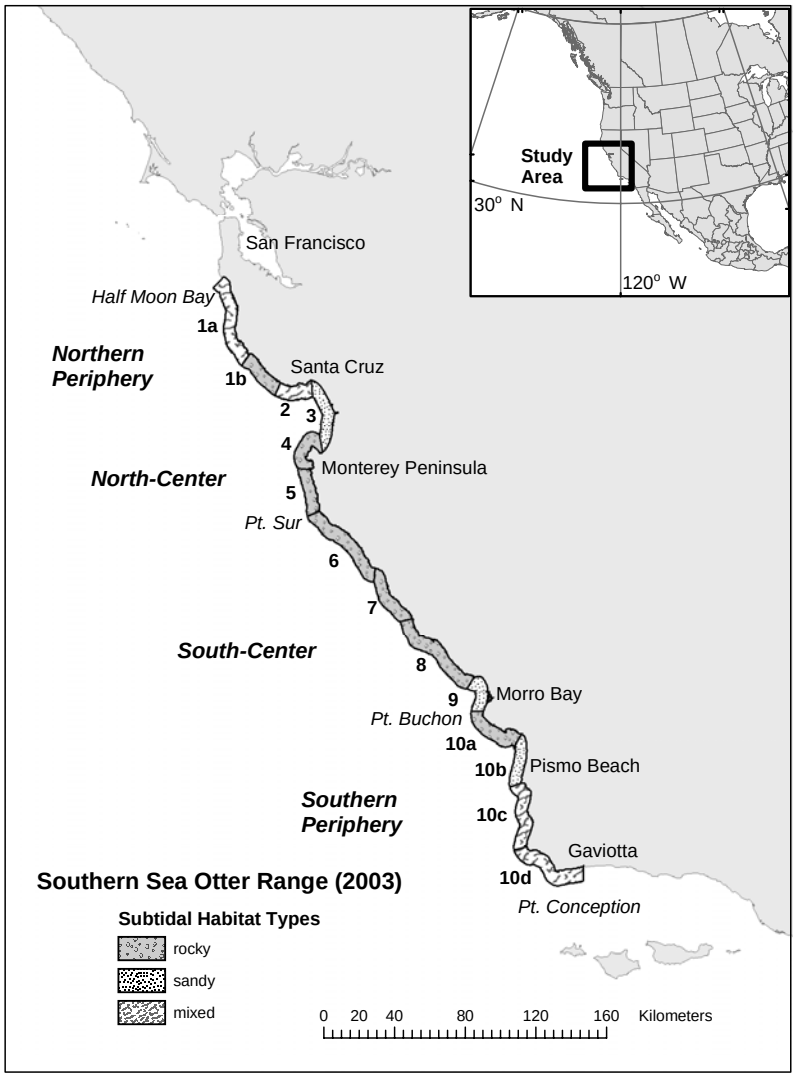

Figure 3. Range of the southern sea otter along the mainland coast of California (range limits based on 2003 survey data) divided into 14 sections of similar sub-tidal habitat (Laidre et al. 2001). These sections were used as fundamental geographical units for our analysis of spatial variation in demography, although the northern-most units (1a and 1b) and the southern-most units (10a, 10b, 10c and 10d) were collapsed into sections 1 and 10, respectively, in order to achieve sufficient carcass sample sizes for each of the 10 remaining coastline sections. Also shown are 4 broader geographical sub-divisions: the northern periphery (consisting of coastline section 1), north-center (sections 2-5), south-center (sections 6-9) and southern periphery of the range (section 10).

We incorporated spatial variation in survival by defining discreet geographic areas: specifically, we divided the sea otter's range in California into different regions within which demographic rates were assumed to be constant, but between which rates were assumed to vary. The locations of boundaries between groups, and the actual number of groupings, were treated as unknowns to be determined by maximum likelihood analysis. To make this fitting manageable, we first divided the current range of the southern sea otter into 10 contiguous coastline segments (Figure 3), corresponding to areas of similar habitat type (Laidre et al. 2001). Because the average length of the 10 coastline segments corresponded roughly to the size of the annual home range of a single adult female sea otter (Ralls et al.

1996), we considered further sub-division unnecessary. Spatial groups (g) were next defined as sets of one or more of these coastline segments: we did not require that all coastline segments within a group be geographically contiguous. For example, assuming only two group levels (g = 1 or 2), three of the 46 possible schemes to be evaluated would be:

i)	1	1	1	1	1	2	2	2	2	2
ii)	1	2	2	2	2	2	2	2	2	2
iii)	1	2	2	2	2	1	1	1	1	1

Each postulated grouping scheme was exclusive (i.e. every one of the coastline segments was assigned to one and only one group), and all possible permutations of up to four groups were considered. For models with two group levels, the effect of location on survival was incorporated using the function:

$$f_g = B \cdot \theta_{17} + B \cdot x \cdot \theta_{18} + B \cdot y \cdot \theta_{19} + B \cdot t \cdot \theta_{20} + B \cdot x \cdot y \cdot \theta_{21} + B \cdot x \cdot t \cdot \theta_{22} + B \cdot y \cdot t \cdot \theta_{23} + B \cdot x \cdot y \cdot t \cdot \theta_{24} \quad \textbf{6}$$

where B is a switch variable: $B = 1$ if $g = 2$ and $B = 0$ if $g \neq 2$. Equation 6 allows for interactions between the location effect and age, sex and time effects. By adding additional switch variables (and thus additional fitted parameters), we could allow for three or four grouping levels. We considered the location of each spatial breakpoint to be a fitted parameter: thus example i, above, would require 1 additional parameter (specifying the breakpoint between coastline segment 5 and 6), while example iii would require 2 additional parameters (specifying breakpoints between coastline segment 1 and 2 and between coastline segment 5 and 6).

The probability of a mature female sea otter producing an independent juvenile is the product of two vital rates, the birth rate (b) and the weaning success rate (w, defined as the probability that an offspring will be successfully reared from birth to weaning at 6 months, conditional upon survival of the mother). Because previous studies suggest that b is relatively invariant within and between sea otter populations, we set b as a constant, while allowing w to vary. The age of first reproduction reported for southern sea otters ranges from 2 to 5 years, with most females producing their first pup by age 3 (Sinha et al. 1966, Jameson and Johnson 1993, Riedman et al. 1994). Published estimates of the birth rate for southern sea otters range from 0.88 to 1.07, depending on the method of calculation (Siniff and Ralls 1991, Eberhardt and Schneider 1994, Riedman et al. 1994, Eberhardt 1995). We set the age of first reproduction to 3 years, and the annual birth rate for mature females to 0.9 (Riedman et al. 1994).

Weaning success in sea otters can vary considerably, unlike birth rates, and has been shown to be age dependant, with older females successfully rearing a greater proportion of pups to independence (Riedman et al. 1994, Monson et al. 2000b). For our analysis, the only means of fitting weaning success rate was to compare predicted with observed total pup counts.

Although annual pup counts provide sufficient information with which to detect changes in reproductive success at the level of the population, they are not alone sufficient to estimate age-specific patterns of reproductive success. Our solution to this problem was to start with a baseline vector of age-specific weaning success rates (w', derived from previously published data) and then allow w' to be adjusted up or down by a modifying function, which could be fit to the raw data. Our baseline values for age-specific weaning success were derived from data reported by Riedman and Estes (1994). To create a smoothed w' vector, we fit a single-parameter logit function to their point estimates:

$$w'_x = \frac{e^{\gamma \cdot x^2}}{1 + e^{\gamma \cdot x^2}} \qquad \textbf{7}$$

where γ is the fitted parameter (γ = 0.01548, 95% CL = 0.0096–0.0213). Equation 7 produced a good fit to the published data ($R^2 = 0.823$), and resulted in an increasing, S-shaped curve approaching 1 for females aged > 10 years. Realized weaning success, w, was then calculated as the product of the baseline vector, w', and a modifying function:

$$w_{x,t,g} = w'_x \cdot \left(0.5 + \frac{e^{\theta_{25} + t \cdot \theta_{26} + B \cdot \theta_{27}}}{1 + e^{\theta_{25} + t \cdot \theta_{26} + B \cdot \theta_{27}}} \right) \qquad \textbf{8}$$

where B is a spatial switch variable, as defined for equation 6 (the same spatial grouping levels, g, were used for weaning success and survival). As shown, equation 8 allows for both a continuous time effect and a categorical location effect (with two spatial grouping levels). We also evaluated categorical time effects (equivalent in form to equation 5), and allowed for up to four spatial grouping levels by adding additional switch variables (and thus additional fitted parameters).

The functions shown in equations 3, 4, 5, 6 and 8 can each be modified by adding or removing individual terms, or simplified to a single parameter, or even set to equal 0 (in which case survival and weaning success become a function of age only, with no sex, time or location effects). Each unique combination of functional forms, in conjunction with each unique spatial grouping scheme, represents a hypothetical model of demographic variation in the southern sea otter between 1992 and 2001: we will hereafter refer to a particular model form as M_i (i =1, 2…I, where I is the total possible number of unique model forms). Each unique model, M_i, will have an associated vector of model parameters, $\boldsymbol{\theta_i}$ ($\boldsymbol{\theta_i} = [\theta_1, \theta_2 \ldots \theta_n]$); the length of vector $\boldsymbol{\theta_i}$ will vary from the simplest model (n=4) to more complex models (n>50). Note that the estimates of survival and weaning success are not themselves model parameters, but are derived from the output of the model. Thus for model M_i, each unique combination of parameter values will result in a unique set of survival and weaning success estimates.

Matrix projection: calculation of expected carcass distributions and population counts

We used a highly modified age-classified Leslie matrix (Leslie 1945) to model population dynamics over the study period (T = 11 years, from 1992 to 2002), classifying animals by age, sex, and spatial grouping (Schoen 1988). We did not consider immigration or emigration (probability of transition between spatial groupings was set to 0). One useful characteristic of population matrices is that initial stationary age-distribution vectors and vital rate sensitivities and elasticities can be rapidly derived using standard algebraic techniques (Caswell 2001). Another key advantage for our analysis is that changes in the age-distribution and abundance of the living population, as well as expected numbers of age-classified carcasses produced over a specified time period, can be easily calculated as the product and by-product (respectively) of matrix multiplication with an age-classified population vector. Starting with the number of otters, N, in a particular year class (x) and sex class (y), at a particular time (t) and within a particular spatial grouping (g), we calculated the expected number surviving to time t+1 as:

$$N_{x+1,y,t+1,g} = N_{x,y,t,g} \cdot s_{x,y,t,g} \qquad \textbf{9}$$

and we calculated the associated expected number of carcasses produced as:

$$D^{\exp}_{x,y,t,g} = N_{x,y,t,g} - N_{x+1,y,t+1,g} \qquad \textbf{10}$$

Equation 10 was used to create the sex-, time- and location-specific vectors of expected carcass age distributions used in the Maximum Likelihood Analysis (see below).

Equation 9 was used to calculate the expected numbers of independent otters at time t+1 for all year classes but the first: the expected numbers of animals entering the youngest year class at time t+1 were calculated as the summed reproductive output of all females in an area between t and t+1. In the interest of simplifying matrix projections, we combined the vital rates b and w in order to express reproduction as $R_{x,t,g\to y}$, the probability of a female of year class x in spatial group g at time t successfully producing a 0-year-old recruit of sex y that was alive at time t+1. The simplest approximation for a birth-flow population would be to consider a "typical female" that gives birth exactly half way through the year (Caswell 2001): for such an individual, $R_{x,t,g\to y}$ would be calculated as $\frac{1}{2} \cdot b_x \cdot w_{x,t,g} \cdot s_{x,0,t,g}$ (i.e. assuming 50:50 sex ratio, and accounting for the birth, weaning and survival probabilities for the mother). However, because we wished also to keep track of the expected number of dependant pups at time t+1 (for comparison with the annual pup counts), we instead divided $R_{x,t,g\to y}$ into two components: $R^{1}_{x,t,g\to y}$ the probability of producing a pup that successfully weans and survives as an independent juvenile at t+1, and $R^{2}_{x,t,g\to y}$, the probability of producing a pup that is still dependent during the census at t+1. The first probability accounts for females that pup during the first six months after the census, while the second accounts for females that pup during the six months prior to the census: we assume that birth probabilities are divided approximately equally between these two groups.

For the first component of reproduction, $R^1_{x,t,g\to y}$, we consider a typical female to be one that produces a pup exactly 3 months after the census. Such a female must survive for ¾ of the year if her pup is to be weaned successfully, and the weaned pup must then survive for the remaining ¼ of the year as an independent juvenile. We assumed that the post-weaning survival rate was equal to the survival rate for the subsequent juvenile year class, and calculated $R^1_{x,t,g\to y}$ as:

$$R^1_{x,t,g\to y} = \frac{1}{2}\cdot\left(\frac{b_x}{2}\cdot w_{x,t,g}\cdot(s_{x,0,t,g})^{3/4}\cdot(s_{0,y,t,g})^{1/4}\right) \qquad \textbf{11}$$

Calculation of the second component of reproduction, $R^2_{x,t,g\to y}$, was complicated by the fact that the probability of pup mortality is not constant throughout the weaning period (Riedman et al. 1994, Monson et al. 2000b), and thus simply considering a "typical female" (one that pups 3 months prior to the census) would provide a biased estimate of the number of dependent pups present at the census. Detailed longitudinal data on pup survivorship during the 6 month dependency period were only available for Alaska (Monson et al. 2000b), although the general pattern of a rapidly declining mortality rate after birth was consistent with that reported for California (Riedman et al. 1994). The Alaska pup survivorship data were closely fit by the function:

$$l_m = w^{\left(\frac{m}{6}\right)^{1/3}} \qquad \textbf{12}$$

where l_m is the proportion of pups surviving at month m of the 6 month pup dependency period, and w is the mean weaning success rate. Based on the simplifying assumption that the number of pups born each month of the year is approximately equal, we used equation 12 to calculated $R^2_{x,t,g\to y}$ as:

$$R^2_{x,t,g\to y} = \frac{1}{2}\cdot\left(\frac{b_x}{2}\cdot s_{x,0,t,g}\cdot\frac{1}{6}\sum_{m=0}^{5} w_{x,t,g}^{\left(\frac{m}{6}\right)^{1/3}}\right) \qquad \textbf{13}$$

Combining equations 11 and 13, we calculated the number of individuals of sex y entering the 0-year class at time t+1, within spatial grouping g, as:

$$N_{0,y,t+1,g} = \sum_{x=1}^{20} N_{x,0,t,g}\cdot\left(R^1_{x,t,g\to y} + R^2_{x,t,g\to y}\right) \qquad \textbf{14}$$

Equation 13 also allowed us to calculate the expected number of dependent pups that would be counted at time t+1 in spatial grouping g as:

$$P_{t+1,g}^{\exp} = \sum_{y=1}^{2}\sum_{x=1}^{20} N_{x,0,t+1,g} \cdot R^2{}_{x,t,g\to y} \qquad \textbf{15}$$

For the first year of the study period, a population vector was initialized as the product of the observed population count (independents + dependant pups) and the stationary age distribution (SAD) associated with the matrix transition probabilities at t=1. We used the SAD in light of the fact that population growth had been relatively constant for many years prior to the study period (at lambda = 1.05; Figure 2), presumably allowing demographic rates to stabilize. For all subsequent years, we combined the results of equations 9, 14 and 15 to calculate the expected number of independent otters that would be counted at time t+1 in spatial group g as:

$$N_{t+1,g}^{\exp} = \left(\sum_{y=1}^{2}\sum_{x=0}^{20} N_{x,y,t+1,g} \right) - P_{t+1,g}^{\exp} \qquad \textbf{16}$$

Maximum Likelihood Analysis

For any given form of the demographic model, M_i, there are an infinite number of possible combinations of parameter values. The goal of maximum likelihood analysis is to find the single "most likely" set of parameter values, given the observed data sets. Specifically, we want to evaluate the relative likelihood (l) of obtaining the observed counts of independent otters (N^{obs}), dependent pups (P^{obs}), and carcass age distributions (C^{obs}), given the expected counts (N^{exp} and P^{exp}) and carcass age distributions (D^{exp}) predicted by model i with parameter values j (denoted hereafter as $M_{i,j}$)

Following Doak and Morris (1999) we assumed that, given a hypothesized age-at-death distribution, the probability that a randomly selected carcass would belong to year class x (x = 1, 2…20) is described by the multinomial distribution. For each model form and set of parameter values, $M_{i,j}$, we therefore calculated the likelihood of the observed carcass age distribution, C^{obs}, for each sex, time period and spatial grouping, as:

$$\lambda(C_{y,t,g}^{obs} \mid M_{i,j}) = \frac{N!}{C_1!C_2!\Lambda\ C_x!} d_1^{C_1} \cdot d_2^{C_2} \cdot \mathrm{K}\ d_x^{C_x} \qquad \textbf{17}$$

where C_x is the observed number of carcasses in year class x (for all year classes except the first) and d_x is the expected proportion of carcasses in year class x, calculated simply as $D_x/\sum D_x$. Equation 17 was solved separately for each sex, year and spatial grouping: the relative likelihood of model $M_{i,j}$ over all sexes, years and spatial groupings is equivalent to the product of the l ($C^{obs} \mid M_{i,j}$) estimates.

To calculate the relative likelihood of observed population counts, we assumed that the deviations between observed and expected counts were primarily due to observer error,

rather than process error, and that the deviations were log-normally distributed (Hilborn and Mangel 1997). We let the variance in counts of independent otters be represented by σ_N^2, and the variance in counts of pups be represented by σ_P^2 (these represent additional fitted parameters). For each model form, $M_{i,j}$, we calculated the likelihood of observed counts of independents, N^{obs}, as:

$$\lambda(N^{obs} \mid M_{i,j}) = \frac{1}{\sqrt{2 \cdot \pi \cdot \sigma_N^2}} \cdot e^{\left(-1 \cdot \frac{(N^{obs} - N^{\exp})^2}{2 \cdot \sigma_N^2}\right)} \qquad \textbf{18}$$

and we calculated the likelihood of observed counts of pups, P^{obs}, as:

$$\lambda(P^{obs} \mid M_{i,j}) = \frac{1}{\sqrt{2 \cdot \pi \cdot \sigma_P^2}} \cdot e^{\left(-1 \cdot \frac{(P^{obs} - P^{\exp})^2}{2 \cdot \sigma_P^2}\right)} \qquad \textbf{19}$$

As with equation 17, equations 18 and 19 were solved separately for each year and spatial grouping and then multiplied to obtain an overall likelihood estimate.

The net likelihood of $M_{i,j}$ is equivalent to the combined probability of obtaining the observed carcass age distributions and population counts across all years and spatial groupings, and thus must be calculated as the product of the product of equations 17, 18 and 19 over all time periods and spatial groupings (and in the case of 17, for both sexes). To simplify calculations, and following standard practice, we converted all likelihood values to negative log-likelihoods ($\boldsymbol{L}$ = -log(l)) and instead calculated the sum of the associated $\boldsymbol{L}$ values (Hilborn and Mangel 1997). The maximum likelihood solution for the best parameter estimates for model M_i was obtained by minimizing the total $\boldsymbol{L}$. To perform model fits we used a box-bounded, global optimization routine based on the DIRECT modification of the Lipschitzian minimization algorithm (Jones et al. 1993). Note that we did not weight the two data sets (carcass age structure and population counts) according to their expected variability (but see Pascual et al. 1997) because the un-weighted likelihood values provided reliable results using simulated data sets with a wide range of introduced observer error.

Incorporating model uncertainty

Maximum likelihood analysis provided the optimal set of parameter values for each unique model form, M_i; however, we had no *a priori* information with which to judge which single model (or sub-set of models) would provide the best approximation to reality. Naturally the models with more parameters provided better fit to the data and thus had smaller values of $\boldsymbol{L}$, but this measurement alone provides a poor indication of the robustness or utility of a particular model (Hilborn and Mangel 1997). We used information theory criterion to compare and select models, and to formally account for model uncertainty in our final, overall estimates of demographic parameters (Burnham and Anderson 1998).

For each model form, M_i, we calculated an associated AIC value (Akaike 1973):

$$AIC_i = 2 \cdot L_{i,\min} + 2 \cdot n_i \qquad \textbf{20}$$

where $\boldsymbol{L}_{i,min}$ is the minimum negative log-likelihood value and n_i the number of parameters for model M_i. The AIC value provides an unbiased method for comparing both nested and non-nested model forms, penalizing models with large numbers of parameters (Akaike 1973). The best-supported model, given the data at hand, has the lowest associated AIC value, AIC_{min}. However, to consider only the single best model (out of all possible models) is to ignore uncertainty: put another way, if there were a replicate data set for the time period in question, it is quite possible that the AIC_{min} for the replicate data would be associated with a different model form. To account for this uncertainty, we calculated Δ_i for each model ($\Delta_i = AIC_i - AIC_{min}$), following Burnham and Anderson (1998). Models with low values of Δ_i are well supported by the data, while models with high values of Δ_i have very little support (that is, they provide a very poor approximation to the existing data). We limited our consideration to the sub-set of Z models having Δ_i values below a cut-off value, Δ_{crit}, which we initially set to 10 (Burnham and Anderson 1998). Finally, for each of the Z models considered, we calculated Akaike weights, α_i as:

$$\alpha_i = \frac{e^{-\frac{1}{2}\Delta_i}}{\sum_{i=1}^{Z} e^{-\frac{1}{2}\Delta_i}} \qquad \textbf{21}$$

The α_i values sum to 1 for the Z models, and represent a measure of the relative level of support for model i (Burnham and Anderson 1998).

The vast number of possible spatial grouping permutations that could be included in our model formulation presented a severe computational challenge. Rather than finding maximum likelihood solutions for every possible combination of functional form and spatial grouping scheme, we used an iterative selection approach to limit the number of grouping schemes considered. First, for a subset of 20 functional forms for other model variables (i.e. those 20 functional forms that provided the best fit to the data with no spatial groupings), we conducted maximum likelihood analysis for all combinations of spatial grouping schemes. We then summed α_i values across all models that included each of the 9 possible break points (i.e. the 9 boundaries between the 10 coastline sections), and used α_i sums as an indication of the relative support for each breakpoint. The three breakpoints with most support each had over 15% of the summed α_i, for a total of 61%, while all other breakpoints had less than 10% (Figure 4). We conducted all subsequent analyses using the 15 spatial grouping schemes that included all or a sub-set of these three breakpoints. The total number of model forms evaluated was 35,178, which included all combinations of the 15 spatial groupings and biologically plausible formulations of f_x, f_y, f_t, and f_g. We then applied Δ_{crit} to identify the Z models to be used for subsequent analysis.

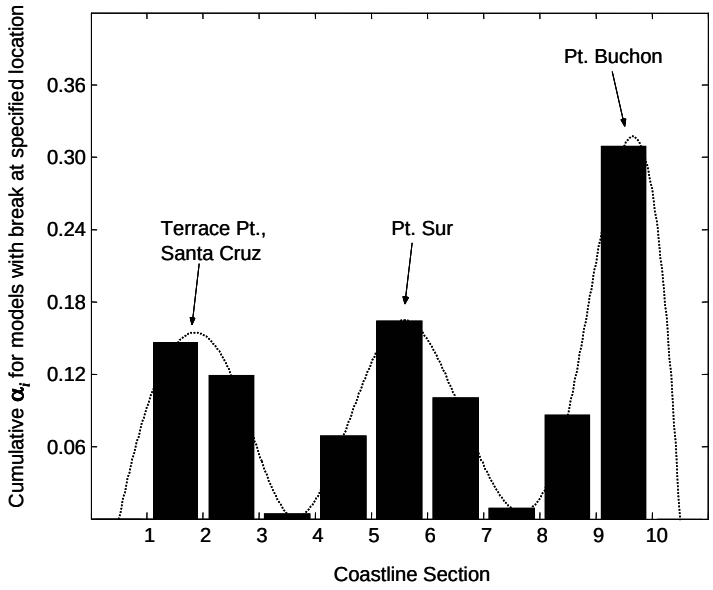

Figure 4. The relative degree of model support for all potential arrangements of 10 coastline sections into areas of similar demography. Summed AIC weights (α_i values) are shown at each potential break-point: the three peaks of the resulting distribution correspond to the best-supported break locations.

We next calculated model-averaged estimates of all demographic rates, as well as the associated unconditional variance estimates. To simplify presentation, we let $\hat{S}_i$ represent the estimated survival for a sea otter of age x, sex y, at time t and in geographic area g, given the particular set of parameter values associated with the maximum likelihood solution for M_i ($\boldsymbol{L}_{i,min}$). Any set of parameter values other than the maximum likelihood solution will result in an estimate, $S_{i,j}$, which is (by definition) less likely than $\hat{S}_i$, given the observed data. The probability that $S_{i,j}$ is the correct estimate, relative to $\hat{S}_i$, can be obtained using the χ^2 cumulative frequency distribution (with one degree of freedom, assuming only one parameter at a time is varied, Hilborn and Mangel 1997):

$$\Pr(S_{i,j}) \cong \Pr\left(\chi^2_{df=1} \geq 2 \cdot (L_{i,j} - L_{i,\min})\right) \qquad \textbf{22}$$

We sequentially varied each parameter in model M_i, selecting 100 values for each parameter from a uniform random distribution with bounds defined as the best-fit value plus and minus 10% of the best-fit value. This resulted in a set of J survival estimates ($S_{i,j}$) and associated probabilities, calculated using equation 22. We then calculated a model-specific variance estimate for S_i as:

$$\operatorname{var} S_i = \frac{1}{\sum_{j=1}^{J} \Pr(S_{i,j})} \cdot \sum_{j=1}^{J} \Pr(S_{i,j}) \cdot \left(S_{i,j} - \hat{S}_i\right)^2 \qquad \textbf{23}$$

Model-averaged estimates of age-specific survival ($\hat{\bar{S}}$) were calculated (following Burnham and Anderson 1998) as:

$$\hat{\bar{S}} = \sum_{i=1}^{Z} \alpha_i \cdot \hat{S}_i \qquad \textbf{24}$$

Similarly, using the model-specific variance estimates, we calculated unconditional variance estimates as:

$$\operatorname{var}\bar{S} = \left(\sum_{i=1}^{Z} \alpha_i \cdot \sqrt{\operatorname{var} S_i + \left(\hat{S}_i - \hat{\bar{S}}_i\right)^2} \right)^2 \qquad \textbf{25}$$

The model averaged estimates for weaning success rates, as well as their associated unconditional variance estimates, were calculated in an analogous fashion. We evaluated the effect of including more or fewer models by varying Δ_{crit}: this parameter was then set to that value at which further increases produced no significant changes in the model-averaged estimates (i.e. the estimates stabilized to 2 decimal points).

As a graphical evaluation of the goodness of fit of the model estimates of demographic rates, we compared the matrix projection of population growth (using best-fit model to generate vital rates) with the observed population counts for the period 1993–2001. Graphical comparisons of expected and observed population dynamics were made for the population as a whole, and also for 4 major geographic sub-divisions: ordered from north to south, these were 1) the Northern periphery of the range (Half Moon Bay to Santa Cruz); 2) the North-center of the range (Santa Cruz to Point Sur); 3) the South-center of the range (Point Sur to Pt. Buchon); and 4) the Southern periphery of the range (Pt. Buchon to Gaviotta; Figure 2).

Demographic rates and their unconditional variance estimates were calculated for 20 year classes; however, for presentation purposes we collapsed these 20 estimates into 4 broader categories corresponding to descriptive age classes: juveniles (age 0–1 years), sub-adults (age 2–3 years), prime-age adults (age 4–10 years) and old adults (11–20 years). Collapsing the year classes into these age classes facilitated comparisons with survival estimates derived from telemetry-based studies (see below), for which survival is generally estimated by age class rather than year class (Siniff and Ralls 1991). For each age class, *a*, model-averaged estimates for survival and weaning success rates, $\hat{\bar{S}}_a$ and $\hat{\bar{W}}_a$, were calculated by taking the arithmetic means of the survival and weaning rates of the constituent year classes. Variances for each age class were calculated using the Delta method (Hilborn and Mangel 1997), a procedure for calculating the variance associated with a parameter that has been derived from several other variables (in this case, each age class estimate is derived from several year class estimates). We assumed (conservatively) that the estimates for year classes within an age class were highly correlated, specifically that $\rho = 1$, and therefore that the covariance of any two year classes was equal to the square root of the product of their individual variances, leading to an unconditional variance estimate for survival of age class *a* (where *a* consists of *n* constituent year-classes, $x = 1, 2 \ldots n$) of:

$$\operatorname{var}\bar{\hat{S}}_a = \left[\partial\hat{\bar{S}}_a/\partial\hat{\bar{S}}_1 \quad \partial\hat{\bar{S}}_a/\partial\hat{\bar{S}}_2 \quad \Lambda \quad \partial\hat{\bar{S}}_a/\partial\hat{\bar{S}}_n\right] \bullet \begin{bmatrix} \operatorname{var}\bar{S}_1 & \operatorname{cov}\bar{S}_1\bar{S}_2 & \Lambda & \operatorname{cov}\bar{S}_1\bar{S}_n \\ \operatorname{cov}\bar{S}_1\bar{S}_2 & \operatorname{var}\bar{S}_2 & \Lambda & \operatorname{cov}\bar{S}_2\bar{S}_n \\ \mathrm{M} & \mathrm{M} & \mathrm{O} & \mathrm{M} \\ \operatorname{cov}\bar{S}_1\bar{S}_n & \operatorname{cov}\bar{S}_2\bar{S}_n & \Lambda & \operatorname{var}\bar{S}_n \end{bmatrix} \bullet \begin{bmatrix} \partial\hat{\bar{S}}_a/\partial\hat{\bar{S}}_1 \\ \partial\hat{\bar{S}}_a/\partial\hat{\bar{S}}_2 \\ \mathrm{M} \\ \partial\hat{\bar{S}}_a/\partial\hat{\bar{S}}_n \end{bmatrix} \quad \mathbf{26}$$

where $\partial\hat{\bar{S}}_a/\partial\hat{\bar{S}}_x$ was set to 1/*n* for all year classes (i.e. we did not weight by the number of individuals in each year class). Variances for age class-specific weaning success rates were calculated in an analogous fashion.

We calculated 95% unconditional confidence intervals for all estimates using a logit-based "back transform" method (Burnham and Anderson 1998). For a particular parameter estimate, *p*, the lower and upper 95% confidence limits (p_L and p_U, respectively) were calculated as:

$$p_L = \frac{p}{p+(1-p)V}, \quad p_U = \frac{p}{p+(1-p)/V} \quad \mathbf{27}$$

where:

$$V = \exp\left(\frac{Z_{1-0.025}\cdot\sqrt{\operatorname{var}\bar{p}}}{p(1-p)}\right) \quad \mathbf{28}$$

and where $\operatorname{var}\bar{p}$ is the unconditional variance estimate for the parameter in question.

All analyses in Part 1 were conducted using MATLAB programming language (The Math works Inc.), and maximum likelihood function optimization was performed using TOMLAB, a third party optimization program for MATLAB (Holmström 1999).

Part 2: Estimating recent demographic rates (2001-2004)

Between October 2000 and September 2003 we captured and tagged 115 adult sea otters as part of a long-term mark-recapture study of southern sea otters. In order to maximize statistical power for one age class, and based on indications from the carcass record that decreased adult survival might be largely responsible for the faltering recovery of the population as a whole, we intentionally biased our sampling to capture mostly adults: consequently, our sample sizes were too low to present mark-recapture survival data for juveniles or sub-adults.

In general, capture and instrumentation of study animals followed methods described for a previous study (Siniff and Ralls 1991): potential study animals were selected arbitrarily (with the exception of the age-bias mentioned above) and captured by re-breather-equipped divers using "Wilson Traps" (McCleneghan and Ames 1976). Study animals were marked

with color-coded flipper tags, which allow visual identification in the field, and were instrumented with abdominally-implanted VHF radio transmitters (ATS Inc., Isanti, MN) equipped with reliable, medical-grade batteries (Medtronic Inc., Minneapolis, MN). After anaesthetizing the study animals, implant surgeries were performed by qualified veterinarians following a standardized procedure (Williams and Siniff 1983, Monson et al. 2001). A series of standardized data and measurements, including weight, length, tooth condition, and body condition were also obtained from each individual. A reversal agent was used to revive the animals after surgery, and they were immediately released back to their capture locations (usually within 2 hours of their initial capture). All of the radios were equipped with thermal monitors that allowed us to record exact body temperature and/or to detect mortality whenever the animal was in radio contact (mortality was assumed when the internal temperature dropped below 35C, and the carcass was retrieved for necropsy whenever possible).

We partitioned our sampling effort into 3 study areas: 30 females and 13 males were captured at Monterey (north-center of range), 35 females and 12 males were captured at San Simeon (south-center of range) and 25 males were captured at Pt. Conception (southern periphery of range). At Pt. Conception we did not capture females because only males utilize this southern-most portion of the range. All study animals were monitored regularly, both by visual observation and ground-based and/or aerial-based telemetry, for a minimum of 2 years or until they died or disappeared. In the San Simeon study area, shore-based or boat-based observers were able to visually locate study animals 5–7 times per week, allowing for reliable estimates of reproductive parameters (birth rates and weaning success rates) as well as survival. Visual re-sightings were slightly less frequent in the Monterey study area (at least 2 per week), allowing for reliable survival estimates but potentially biased reproductive estimates (Eberhardt and Schneider 1994). Males captured at Pt. Conception tended to move frequently and over great distances throughout the range, making visual observation difficult and highly sporadic; however, twice-monthly range-wide aerial scans (using a Cessna plane equipped with ATS radio-tracking equipment) allowed us to verify location and survival status of these animals. Results from the current study and from a previous study (that utilized identical instrumentation, Siniff and Ralls 1991) indicate that the VHF transmitters were generally reliable for 2 years of deployment. Based on those study animals with precisely-known radio transmitter life spans (N = 25, mean = 756 days, 95% CL = 629–886), there appeared to be a negligible failure rate for the first 18 months post-deployment; consequently, we restrict our analyses to the first 2 years of data for all animals, and treat all disappearances within 18 months of capture as presumptive mortalities. In total, 8 of 41 mortalities (20%) were presumptive and the remaining 33 were confirmed (carcasses were recovered).

We analyzed survival data using a Kaplan-Meier "known-fates" model that allows for staggered entry of study animals (Pollock et al. 1989), and we conducted all computations using Program MARK (White and Burnham 1999). We evaluated a range of model forms, ranging from the simplest possible model (no variation in survival rates) to more complex models that allowed for location effects (study area), sex and time effects, and all possible interactions. Temporal effects evaluated included both study year and seasonal effects, where seasons were defined as winter (January–April), summer (May–August) and fall (September–December). We did not allow for an age effect because all study animals were

considered to belong to a single age class (prime age adults). For each model form evaluated, we calculated AIC values (equation 20) and Akaike weights (α_i, equation 21) and used these to select the best-supported suite of models, limiting consideration to models having Δ_i values below 10. We used model averaging to incorporate model uncertainty into the final estimates (see methods for Part 1, Burnham and Anderson 1998).

We restricted analysis of reproductive parameters to the San Simeon study group, where visual re-sightings were most frequent and where the likelihood of missing unsuccessful reproductive events was minimal. We calculated mean birth rate using the "direct method" (sensu Eberhardt and Schneider 1994):

$$\bar{b} = \frac{1}{K}\sum_{k=1}^{K} b_k \left(\frac{365}{N_k}\right) \qquad \textbf{29}$$

where K is the total number of females monitored for at least 365 days, b_k is the number of observed births observed for female k, and N_k is the number of days female k was monitored. For weaning success, we considered all pups with a dependency period of 120 days or more to have been weaned successfully (Riedman et al. 1994), and estimated mean weaning success across females.

All estimates reported in the text are followed by 95% confidence intervals (CI_{95}) and the error bars in figures represent ± 1 standard error (unless otherwise indicated). With the exception of the birth rate and weaning success rate estimates derived from mark-recapture data, model-averaged estimates are reported throughout, and confidence intervals and standard errors reflect unconditional sampling variances. The relative degree of support for specific model effects is represented by the summed AIC weights ($\Sigma\alpha_i$) of all model forms in which the effect was present.

Results

Part 1: Past demographic rates (1992-2001)

There were 210 model forms having $\Delta_i \leq 10$; however, after sorting models by their AIC values (from lowest to highest), α_i values were found to be extremely low (≤ 0.005) for all but the first 35 models (Figure 5). Reducing $\Delta_{i,crit}$ (the cut-off value for model consideration) down to 5 had no measurable effect on model-averaged vital rate estimates; we therefore re-set $\Delta_{i,crit}$ to 5, restricting subsequent analyses to the 34 best-supported models (Appendix A).

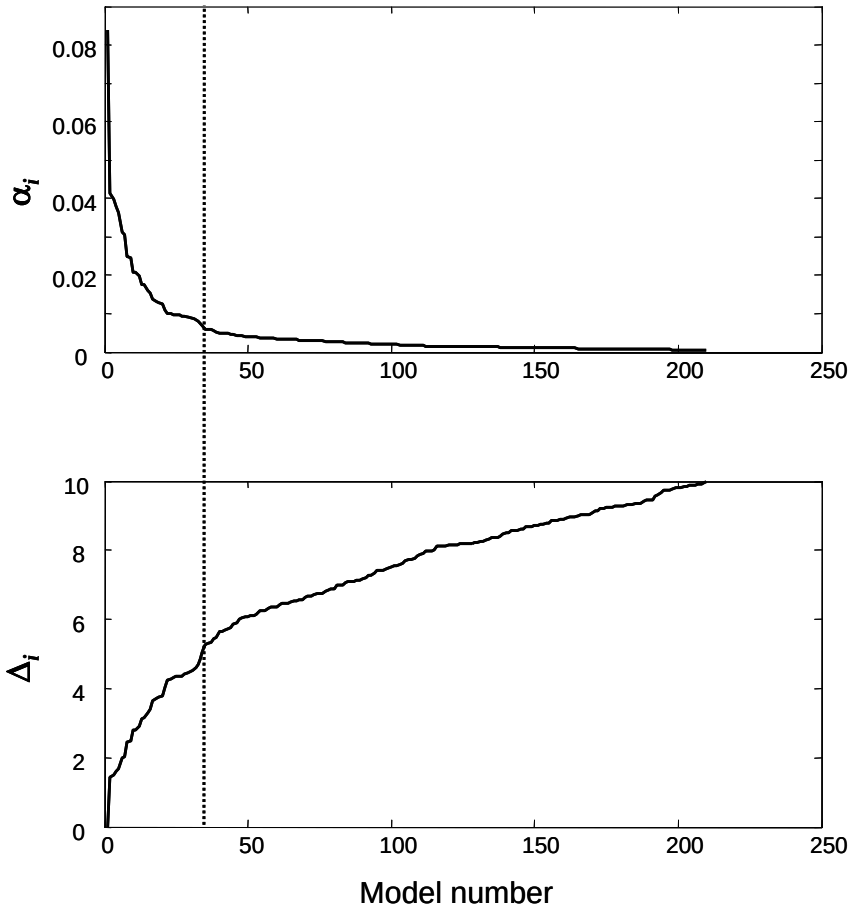

Figure 5. Profiles of AIC weights (α_i values, top graph) and Δ_i values (bottom graph) for the 210 models with $\Delta_i \leq 10$. The α_i values approach an asymptote after model 35 (indicated by dotted line), which also corresponds to the final cut-off value ($\Delta_i = 5$) used to select models for inclusion in model averaging.

The model-averaged estimates of age-specific vital rates lead to a demographic schedule that is consistent with previous models (Siniff and Ralls 1988): annual survival was low for juveniles, increased to a maximum for animals aged 4–8 years, and then decreased gradually for older adults (Figure 6). Female survival was higher than that of males at all ages and an age-sex interaction was present in 32% of models ($\Sigma\alpha_i = 0.23$), resulting in an accelerated decrease in survival with age for males as compared to females: such a pattern is consistent with the female-biased sex ratio reported for southern sea otters (Jameson 1989). In general, the model results indicated similar temporal and spatial trends in survival for males and females (Appendix B), but because changes in male survival rates have little effect on population growth (Caswell 2001) we report all further results for females only.

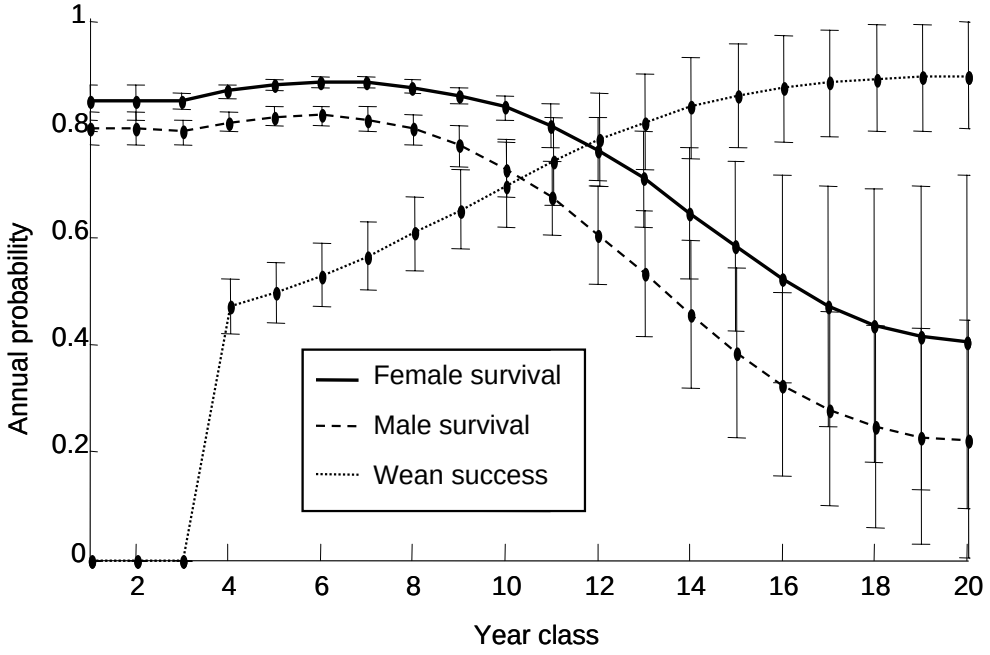

Figure 6. The Age-specific schedule of annual survival rates for females (solid line) and males (dashed line), as well as weaning success rates (dotted line). Model-averaged estimates and their standard errors are shown for 1992 in the north-center of the range.

In 26% of models ($\Sigma\alpha_i = 0.20$) the weaning success rate was lowered from the baseline, but was un-adjusted in all remaining models. For adult females, the model-averaged estimate of weaning success was 0.61 (CI_{95} = 0.48–74). There was little (if any) support for either spatial or temporal variation in weaning success: 1 of the 34 models considered included an increase in weaning success with time ($\Sigma\alpha_i = 0.01$), and none of the best-supported models included a spatial effect.

In contrast to weaning success rates, survival rates were variable over both space and time (a comprehensive table of model-averaged survival rates is provided in Appendix B). Almost all models considered (97%, $\Sigma\alpha_i = 0.95$) included a spatial effect, and while there were several possible grouping schemes (Appendix A), the common pattern in all cases was lower survival in the north-center of the range. Survival rates were somewhat higher in the northern periphery and south-center of the range, and were highest at the southern periphery of the range (Figure 7). The majority of models also included a time effect (65%, $\Sigma\alpha_i$ = 0.60), which took the form of a decrease in survival rates over the study period: for example, adult female survival in the north-center of the range was 0.87 (CI_{95} = 0.83–90) in 1992 but decreased to 0.84 (CI_{95} = 0.77–89) in 2001. Although the nature of the temporal change was continuous in many of these models ($\Sigma\alpha_i = 0.32$), there was also substantial support for a categorical time effect ($\Sigma\alpha_i = 0.28$), suggesting a sudden drop in survival between 1994 and 1995 (Figure 8). Models with a categorical time effect (as opposed to a continuous effect) were penalized for having an additional parameter (θ_t, the location of the temporal break), thus the degree of support for a sudden drop in survival in the mid 1990's is unlikely to be spurious.

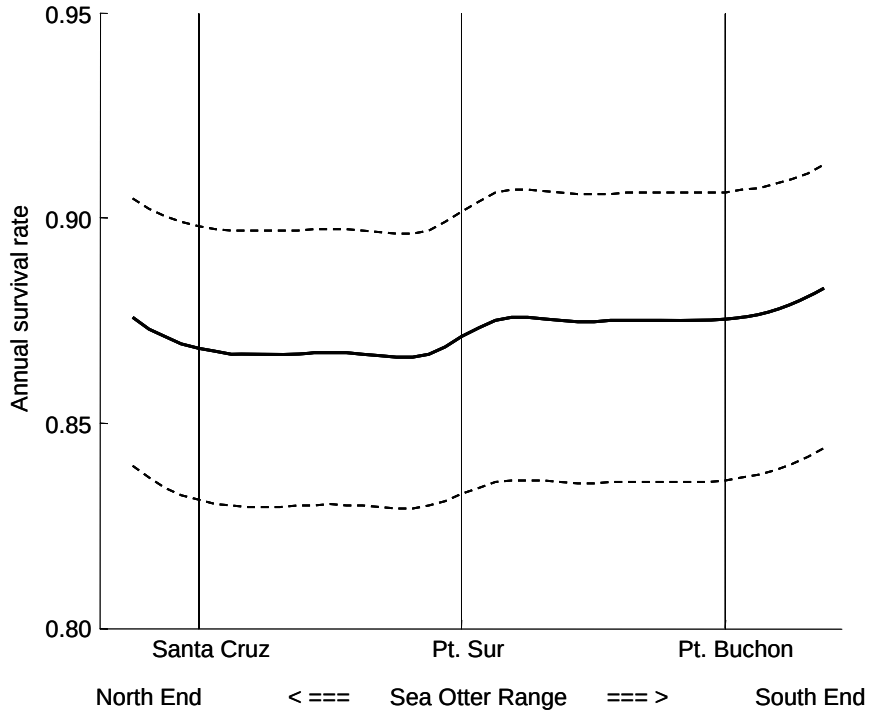

Figure 7. Spatial variation in the annual survival rate of adult females. Center curve shows the model-averaged rate for 1992, while dashed lines indicate the unconditional 95% confidence bounds.

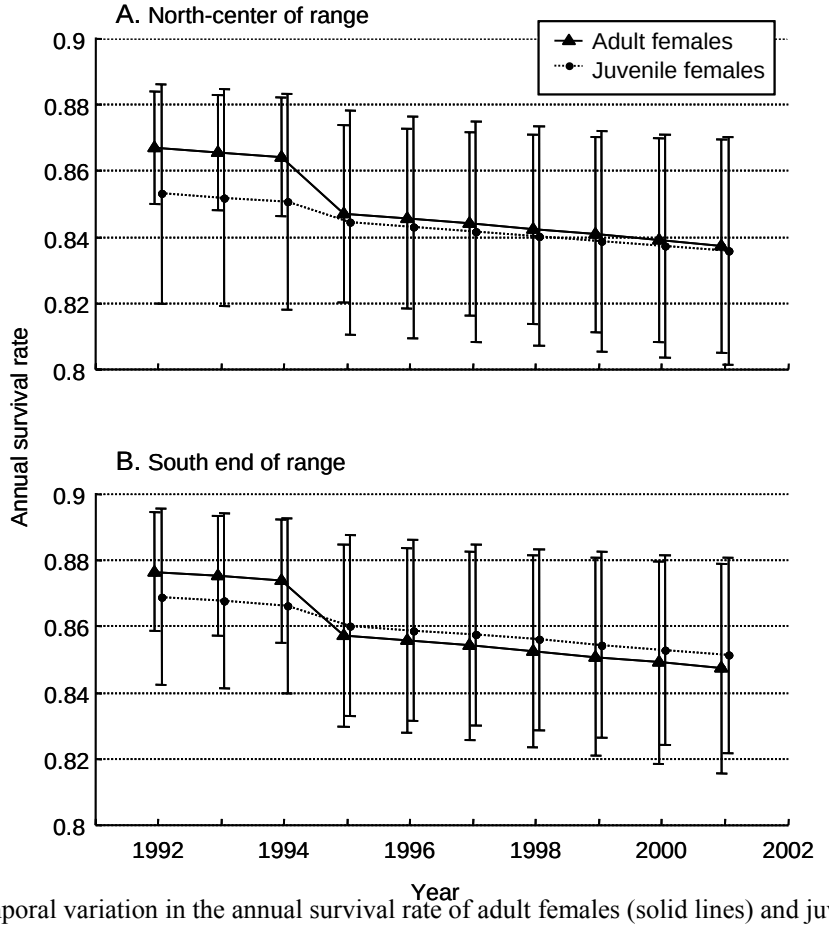

Figure 8. Temporal variation in the annual survival rate of adult females (solid lines) and juvenile females (dashed lines). A) Estimated survival rates for 1992-2001 in the north-center of the range; B) estimated survival rates for 1992-2001 in the southern periphery of the range.

The spatial and temporal trends in survival were similar but not identical for all age/sex classes: 38% of the models considered ($\Sigma\alpha_i = 0.36$) included interaction effects of some kind. Three interactions were most common: juvenile and sub-adult survival tended to be relatively higher in the southern half of the range, the decrease in survival over time was not as pronounced in the south, and the temporal change in survival was relatively greater for older animals, such that the model-averaged adult survival rates tended to converge with juvenile survival rates by 2001 (Figure 8). The proportional decrease in survival between 1992 and 2001 was greatest for old adults; however, given the age-specific patterns of matrix elasticity values (Figure 9), decreased survival of prime-age adults likely contributed most to the observed change in population growth over the 1990's.

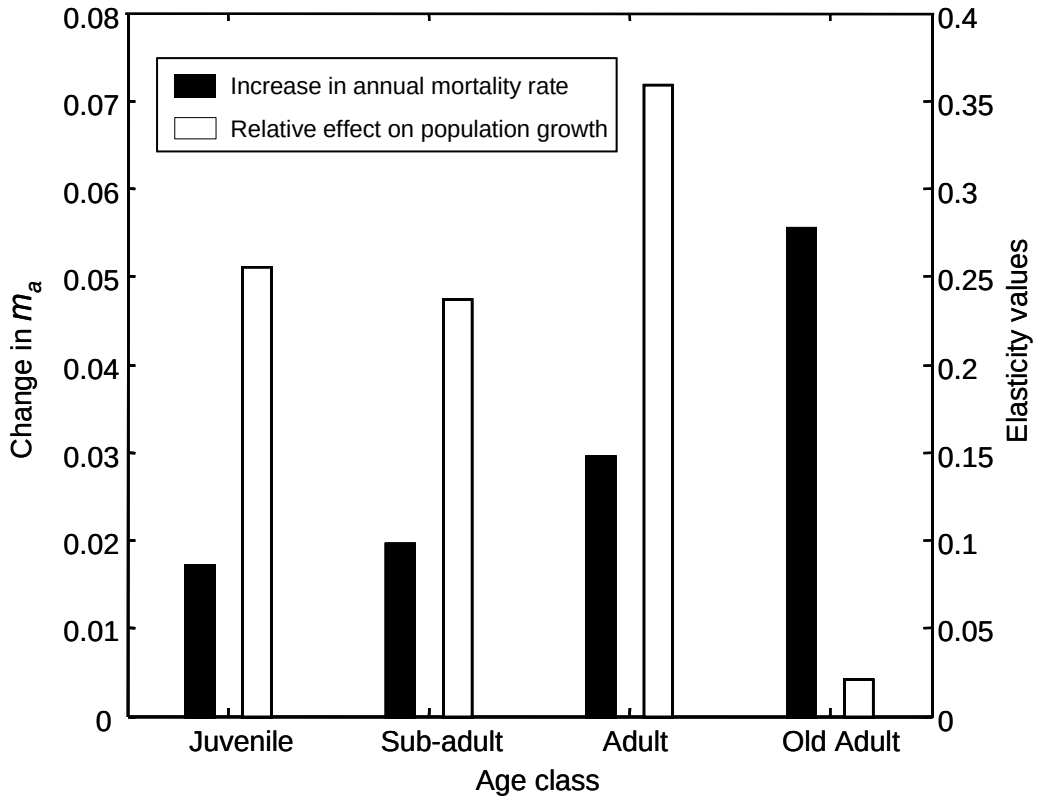

Figure 9. Increase in annual mortality rates ($m_a = 1 - S_a$) between 1992 and 2001 (black bars) and corresponding survival elasticity values (white bars) for 4 female age classes: juveniles, sub-adults, adults and old adults. Elasticity values were derived algebraically from the 1992 matrix and summed for each age class.

The model-averaged estimates of vital rates resulted in a relatively close match between expected and observed population growth, when compared at the level of the entire population (Figure 10A). Interestingly, there was greater disparity between expected and observed counts when plotted separately for the four major geographic regions (Figure 10B). However, the greatest discrepancies were between expected and observed counts in the south-center and southern periphery of the range, and annual discrepancies were strongly and negatively correlated for these two areas ($\rho = -0.82$, $P = 0.002$), suggesting that the disparities reflect (to a large degree) the movement of animals between regions.

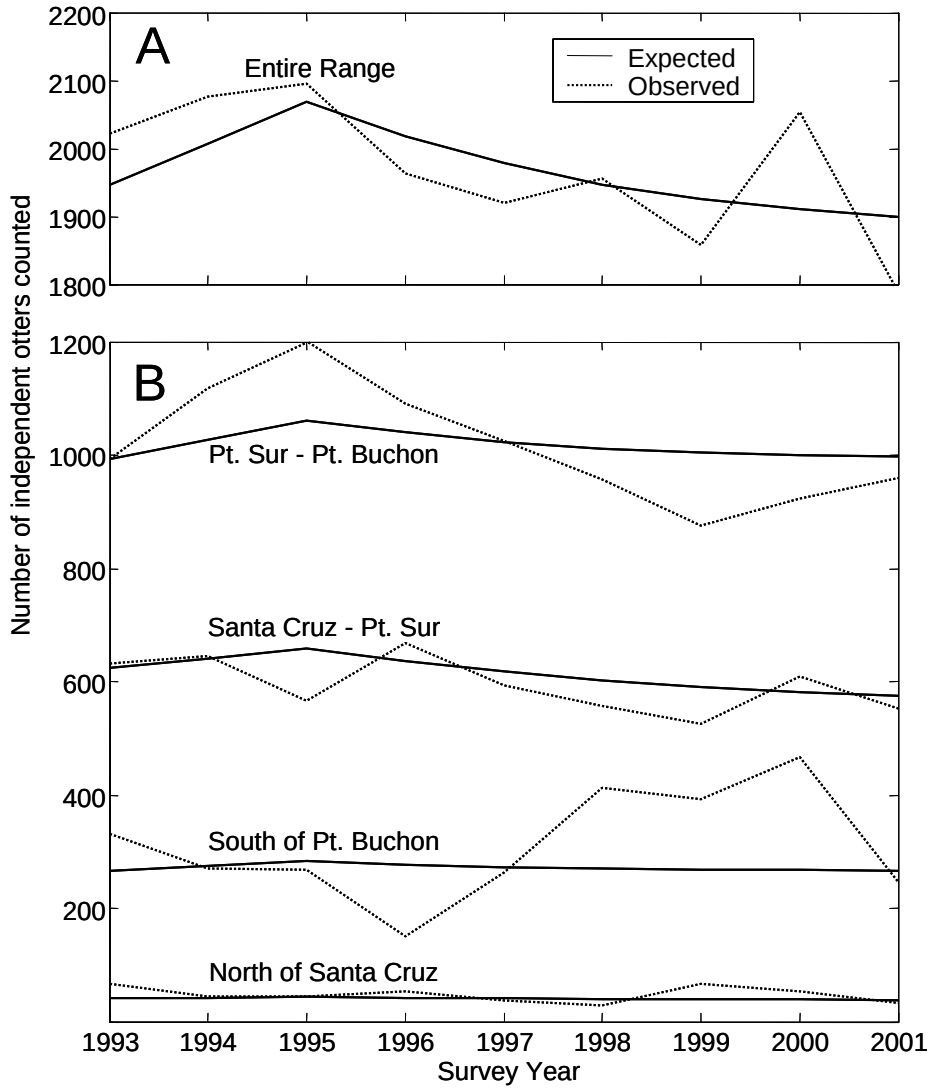

Figure 10. Expected trends in population abundance between 1993 and 2001, as predicted by matrix projections using the maximum likelihood estimated vital rates. Observed population counts are plotted for comparison. A) Expected vs. observed counts for the entire population; B) expected vs. observed counts for 4 major geographic sub-divisions of the range.

Part 2: Recent demographic rates (2001-2004)

In total, 27 adult females were monitored for at least 365 days and were used for estimation of reproductive rates. The average monitoring period was 628 days per female, for a total of 16,950 monitoring days, and 46 pups were produced within this period. Although pups were produced year-round, the frequency of pup births was higher between September and February (n = 35) than between March and August (n = 11). Individual females produced an average of 0.98 pups·yr^{-1} (standard error = 0.059, CI_{95} = 0.86–1.09) and had a mean weaning success rate of 0.61 (standard error = 0.088, CI_{95} = 0.57–0.65). Both birth and weaning success rates were slightly higher than the equivalent rates reported for the 1980s (0.90 and

0.57, respectively: Siniff and Ralls 1991), although these differences were not statistically significant.

The survival analysis resulted in 10 model forms having $\Delta_i \leq 10$. The two best-supported models ($\Sigma\alpha_i = 0.71$) included both a location effect and a seasonal effect, but no variation due to sex or study year (Appendix C). There was overwhelming model support ($\Sigma\alpha_i = 0.80$) for a difference in survival between the center of the range (Monterey and San Simeon study areas) and the Pt. Conception study area, but very little support ($\Sigma\alpha_i = 0.02$) for a difference between Monterey and San Simeon. Animals from Pt. Conception experienced higher survival than animals from the center of the range (Table 1), consistent with the spatial patterns reported in Part 1 (Figure 7). In the Monterey and San Simeon study areas, survival during the summer months was lower than fall and winter (Figure 11); this trend was not evident in the Pt. Conception study area, where summer survival rates were either identical ($\Sigma\alpha_i = 0.42$) or slightly higher ($\Sigma\alpha_i = 0.54$) than fall and winter survival rates.

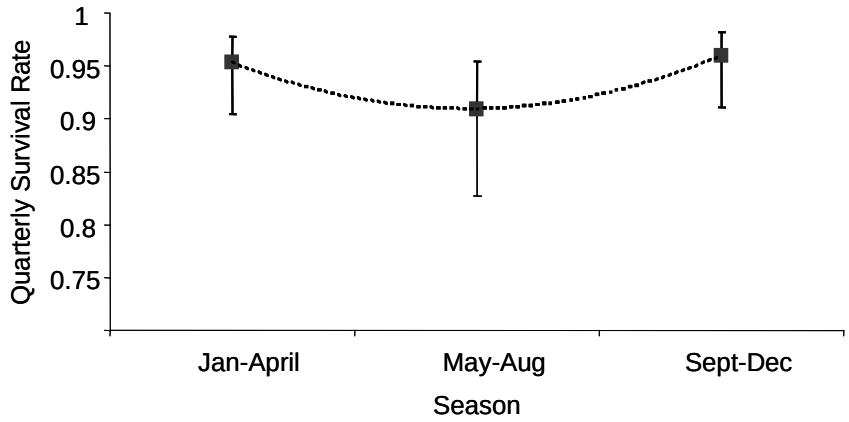

Figure 11. Seasonal variation in survival probabilities for adult females in the center of the range, as estimated from mark-recapture data. Model-averaged estimates of quarterly survival are shown, spanned by their 95% confidence intervals.

The recent survival rates reported here for adult females are considerably lower than the estimates reported from the 1980's (Table 1), even though both studies used identical methodologies and spanned the same geographical range. The trend for males is somewhat different, apparently having increased since the 1980's (Table 1). Combining the recent survival estimates and the 1980's estimates (both derived from mark-recapture data) with the estimates for the 1990's (derived from carcass age-distributions and census counts; Part 1) provides a consistent and comprehensive picture of temporal variation in adult female survival (Figure 12).

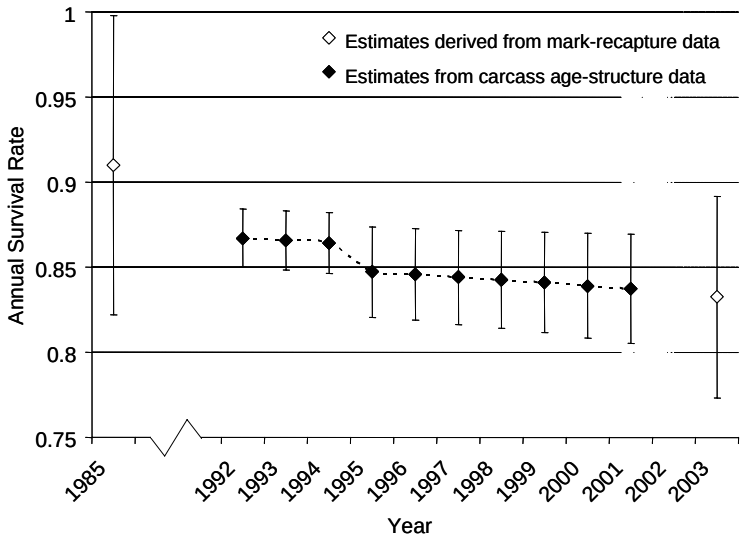

Figure 12. Synthesis of survival estimates derived from two independent analyses and data sets, summarizing the inferred temporal changes in adult female survival in the center of the range. The 1985 estimate is that reported by Siniff and Ralls (1991).

Table 1. Maximum Likelihood model-averaged estimates of annual survival rates for adult sea otters, derived from telemetry-based, mark-recapture data

Sex/Study Group	Mean	SE	L95	U95
Females				
1984-86, Center of Range 1	0.91	0.088	-	-
2001-03, Monterey peninsula	0.832	0.059	0.683	0.917
2001-03, San Simeon	0.831	0.060	0.682	0.916
Males				
1984-86, Center of Range 1	0.61	0.167	-	-
2001-03, Monterey peninsula	0.833	0.060	0.683	0.918
2001-03, San Simeon	0.833	0.060	0.681	0.918
2001-03, Pt. Conception	0.864	0.095	0.567	0.956

Discussion

The practical conclusion that can be drawn from the analyses presented here is that average survival rates, particularly survival of prime-aged adult females in the north-center of the range, decreased substantially over the 1990's, with indication of a sudden drop in survival after 1994 (Figure 12). In contrast to variation in survival rates, it appears that reproduction (birth rates and weaning success) changed very little over the same period. The spatial and temporal trends described here can be used to focus future research on those factors most likely to drive population changes; in particular, factors that impact survival of adult females in the center of the range are of greatest concern. A number of recently identified diseases in southern sea otters, including protozoal encephalitis and idiopathic cardiomyopathy, appear to be responsible for a considerable proportion of the mortality of adult females within the center of the range (Thomas and Cole 1996, Miller et al. 2002, Kreuder et al. 2003), and the proximate and ultimate causes of these diseases should be the subject of further research. We emphasize that the methodological approach described here does not directly test the relative importance of specific factors that may be affecting survival (e.g. diseases, contaminants, fishing gear entanglement); however, our results can be incorporated into sensitivity analyses that do (e.g. Kreuder et al. 2003, Gerber et al. *in press*).

Some of the patterns that emerged from these analyses raise more questions than they answer. For instance, the seasonal variation in survival probability (Figure 11) is difficult to explain, especially considering that the observed pattern – lower survival in the summer – seems to be the opposite of that described for sea otters in Alaska and Russia (e.g. Kenyon 1969, Bodkin et al. 2000). This pattern is consistent, however, with the reported increase in beach-cast carcasses retrieved in summer months during periods of population decline in California (Estes et al. 2003). One explanation for this pattern might be increased incidence of disease in summer, associated with some seasonally-driven environmental factor (e.g. warm water algal blooms). Another possible explanation for a seasonal trend in survival relates to female reproductive status: because there is a higher frequency of pup births in the winter, there must be a corresponding mid-summer peak in the number of females having recently weaned pups. Females generally lose weight throughout the pup dependency period (Monson et al. 2000b), and individuals that are otherwise nutritionally stressed are probably at their poorest body condition immediately post-weaning, at which time they are also generally in estrous and may experience repeated mating interactions with males. The interaction of all these stress factors may cause a mid-summer peak in female mortality; the problem with this explanation is that the seasonal variation in survival appears to affect males equally. A third explanation (not mutually exclusive of the others) pertains to diet profitability: seasonal variation in the nutritional and/or energetic composition of some sea otter prey species is known to occur (related to prey reproductive cycles, e.g. Watt et al. 2000), and may lead to seasonal peaks in the degree of nutritional or energetic stress experienced by some individuals. All of these possible explanations represent testable hypotheses, and further data will be needed to properly evaluate their relative importance. It is worth noting, however, that the latter two explanations can be encompassed by a broader hypothesis of density-dependant population regulation. The seasonal decrease in survival was observed for animals at the center of the range, where re-colonization occurred earliest, densities are highest, and where it might be expected that females would be in poor body

condition and thus subject to stress-related mortality associated with pup weaning and/or variation in prey profitability.

The hypothesis of density-dependant population regulation would seem to be consistent with a number of the trends reported here, including the seasonal variation in survival and the spatial pattern of lower survival in the center of the range (Laidre et al. 2001). There are a number of inconsistencies in this scenario, however, the most important being the age-specific trends in survival (Figure 8). Based on a comparative analysis of sea otter populations in Alaska at varying densities and stages of population recovery, Monson *et al.* (2000b) concluded that density-dependent regulation of sea otter populations occurs primarily as a result of a decrease in weaning success rate and lower juvenile survival, while adult survival varies much less. In contrast, the results presented here for the California population suggest that weaning success has remained unchanged and adult survival has declined more than juvenile survival. These results are perplexing in light of the fact that variation in prime-age adult survival has the greatest potential impact on λ (Figure 9): life history theory suggests that this should be the very stage most buffered by selection (Pfister 1998)[1]. If this is so, then one might reasonably hypothesize that the source(s) of mortality responsible for the reduction in adult survival are "novel" in an evolutionary sense, and not a part of the historical selection regime for this population. Density dependence may indeed be a contributing factor to the current cessation of population recovery, but the age-specific patterns of variation in survival suggest that some density-independent, extrinsic factor (or combination of factors) may also be involved in driving recent trends.

Incorporating the estimated demographic rates into a projection matrix produced expected dynamics that were consistent with observed trends for the population as a whole between 1993 and 2001 (Figure 10A); however, the lack of close fit between expected and observed counts within each geographic region (Figure 10B) were surprising because the logit functions allowed sufficient flexibility to fit even complex patterns of spatial and temporal variation. To some degree this failure to track year-to-year variation in observed counts reflects the constraining influence of the age-structure data, which would tend to "smooth out" short-term variation and instead force the model to track longer-term trends. Another reason for the discrepancies is highlighted by the negatively correlated discrepancies in adjoining areas (Figure 10B), which suggests that some of the variation in counts at the regional level reflects movement of animals between regions, a process not accounted for in our current projection matrix. Movement between sub-populations could (and should) be included in future analyses and management considerations, and data from ongoing telemetry studies (USGS unpublished data) and previous studies of this population (Ralls et al. 1996) can be used to parameterize individual movement rates.

The concordance between the estimates of adult female survival rates derived from multiple data sets and independent analyses (Figure 12) provides strong support for the temporal and spatial patterns indicated by both methodologies (Part 1 and Part 2, above). Perhaps the most perplexing of these patterns is the temporal trend of declining female survival, because this would suggest continued negative population growth in the center of the range, a

[1] Note that the old adult age class actually experienced the greatest decrease in survival, and also has the lowest associated elasticity, consistent with the pattern described by Pfister (1998).

prediction that would seem to be countered by an apparent stabilization of population numbers in recent years (Figure 2). There are only two possible explanations for this discrepancy: the estimates of female survival are biased low (and population growth has in fact stabilized), or else the apparent leveling-off of population counts is misleading. The first explanation seems unlikely given the concordance between independently derived estimates, the substantial sample sizes used for both analytical approaches, and the fact that virtually all the adult females used for the mark-recapture analysis had confirmed fates after two years (thus precluding any bias created by confusing disappearances with mortalities). The second explanation is obviously a great deal more troubling, and raises the question of why the range-wide censuses would fail to reflect a continued decline. Source-sink dynamics could potentially obscure such a trend from detection (Pulliam 1988, Doak 1995) if there were sufficient immigration of animals from the edges of the range, where survival rates are high (Figure 7, Table 1) and population growth is still positive. While this scenario is consistent with the spatial patterns of variation in survival rates and with the extensive northern movements of adult male otters captured at the south end of the range (USGS, unpublished data), further population counts and mark-recapture data will be required to properly test this hypothesis.

In addition to the insights provided about the southern sea otter, two aspects of our methodology have broader implications for population analyses of other species. First, we have described an extension of an existing technique (Doak and Morris 1999, Monson et al. 2000a) that allows for incorporation of additional information, in particular pup counts (which are used to better fit reproductive rates), and for assessment of spatial as well as temporal variation in survival. Secondly, and perhaps more importantly, our general approach to incorporating uncertainty may be applicable to other threatened populations for which there are many possible demographic scenarios to consider, but limited data for analysis and no *a-priori* information with which to identify a few "most likely" scenarios. It is important at this point to emphasize that we are using an information theoretic approach in an exploratory way here; we are not hypothesis testing or striving for a generally applicable model to apply to all situations. The most recognized and definitive reference on information theory and model selection written for ecologists (Burnham and Anderson 1998) is very clear on the dangers of "data dredging", a term that is somewhat vague but could be taken to refer to any approach other than consideration of a small, exclusive set of alternative hypotheses (e.g. a model with *vs*. without a time effect). By this definition, our methodological approach described in Part 1 is in grave danger of violation because we consider such a large suite of possible model forms. We propose that if one can properly account for model uncertainty (i.e. using model averaged estimates and unconditional variances, *sensu* Burnham and Anderson (1998), then a maximum likelihood approach used in this exploratory way can be an appropriate first step towards the elucidation of key demographic processes and spatial/temporal patterns or variation. The approach we suggest can focus attention on a smaller number of well-supported, testable hypotheses about factors underlying observed trends, while helping to divert attention away from other, less important factors. In the case of the southern sea otter, for example, our results provide support for the notion that mortality of males or juveniles at the south end of the range is unlikely to have contributed significantly to the population decline in the 1990's.

Animal populations are influenced by an almost infinite assortment of deterministic and stochastic forces that together affect demographic processes in often complex ways. The vast majority of these forces lead to demographic variation that is immeasurably small and can thus be safely ignored by biologists wishing to model populations to evaluate their viability or select among management options. Statistical hypothesis-testing techniques and model selection criteria are typically used by biologists to reject "insignificant effects" or to select the most parsimonious model or hypothesis (Hilborn and Mangel 1997, Burnham and Anderson 1998). Unfortunately, in most systems there is considerable uncertainty underlying every component of the analysis, and the risks of a wrong decision resulting from such uncertainty are very rarely taken into account (Burgman et al. 1993). We agree with Pascual *et al.* (1997) that a reasonable way of dealing with this uncertainty is to evaluate many alternative models, and then use formal techniques for incorporating the uncertainty into parameter estimates (Burnham and Anderson 1998). Although this may entail sacrificing a certain degree of heuristic simplicity (three alternative model forms are easier to contemplate than 30) as well as precision of the resulting parameter estimates, it may also provide a more realistic picture of the range of potential variation in the study system.

Chapter 3. Temporal and spatial variation in movement patterns

Alisha H. Kage, James A. Estes, M. Tim Tinker, Daniel F. Doak, and Peter T. Raimondi

Abstract

1. The movement of individual animals is well recognized as an important determinant of population dynamics. Understanding how patterns arise and their implications for population dynamics, habitat use, and community interactions are thus important ecological issues. In this analysis, movement data for southern sea otters (*Enhydra lutris nereis*), was compared for temporal and spatial variation between past and current sea otter populations based on several criteria, including average length of movement over several time intervals, average turn angle on successive days, estimates of home range size, and a correlated random walk (CRW) individual based movement model. We hypothesized that the density dependent effect of food limitation on individual behavior may have increased between the 1980s and the present, and if so we would predict that average move length for those animals would increase, turn angles would be less randomly distributed, home range areas would be significantly larger, and a correlated random walk model would more accurately predict daily movement for the past population than for animals occurring in the present population.
2. Overall, individual move lengths did not differ significantly between the 1980s study and the current study. However, there were significant interactions between age/sex classes and time period. Males moved longer distances in the current study (0.18 - 490 km) than they did in the 1980s (0.21 – 111 km), while females had longer overall move lengths during the 1980s (0.02 km – 22 km) than they did during the current study (0.26 km – 15 km).
3. Turn angles for the 1980s population were distributed randomly while turn angles for the current study were not. Contrary to the predicted hypothesis, home range areas for the 1980s animals were significantly larger than those of animals in the current population. As anticipated, data from the 1980s population provided the best fit to the expectations of the CRW model. Data from the current populations did not conform to the model expectations.
4. Factors such as spatial characteristics of habitat (*i.e.* substrate type and bathymetry), along with complex behavioral phenomena such as learning and cultural transmission, likely influence the movement patterns of sea otters. These factors are not accounted for by the basic CRW model. However, the success of describing the movement of one subset of a marine carnivore population using CRW theory provides insight into changes in population status, and will assist in more innovative modeling of individual dispersal, population growth, and range expansion.

Introduction

The movement of individual animals is well recognized as an important determinant of population dynamics. Animals interact with the environment in complex ways, which in turn produce complex movement patterns (Jonsen *et al.* 2003). Most animals rely on movement for finding mates and food, for maintaining thermal conditions, as well as for escaping predation (Bergman *et al.* 2000). Understanding how patterns arise and their implications for population dynamics, habitat use, and community interactions are thus important ecological issues (Jonsen *et al.* 2003).

The study of movement, however, is far behind that of other ecological processes due to the difficulties scientists face both when attempting continuous observation of animal locations and analyzing movement patterns once data have been collected (Turchin 1998). In order to completely describe movement, one must be able to measure the location of an individual continuously. This creates a problem since many animals can not be seen on a regular basis and others can not be seen at all. As a result scientists know little about the spatial ecology of most species of animals and even less about the movement of carnivores (Marsh and Jones 1988).

The need to understand and describe movement is of serious concern to conservationists and managers as they are mandated with the job of designating current and predicting future critical habitat needs for threatened and endangered species. Understanding movement can also provide insight into the social organization and mating systems of different species (Ribble and Salvioni 1990) as well as the manner in which individuals search for spatially dispersed resources (Zollner and Lima 1999). Given this need, models that actually predict movement are of great interest to theoreticians, conservationists, and managers, and quantitative models describing individual movement can be valuable tools for forecasting large-scale spatial distribution patterns and meta-population dynamics (Turchin 1998). Beyond movement *per se*, assessing spatial and temporal patterns of habitat use is fundamental to an understanding of population ecology (Millspaugh and Marzluff 2001). The dynamics of a population are directly linked to the spatial arrangement of individuals (White and Garrott 1990), and at the core of many spatial use analyses is the estimation of an animal's home range (Kernohan *et al.* 2001).

Mammalian carnivores, by nature, are typically rare, secretive, and generally hard to study. It is rare to find a study animal that can be seen on a regular basis once it has been captured and released. However, the California or southern sea otter (*Enhydra lutris nereis*), is an exception. The southern sea otter is a unique marine carnivore because it spends the majority of its life in the nearshore environment along the central coast of California. Because of their nearshore location, and the general coastal accessibility throughout their range, southern sea otters can readily be observed and followed. Moreover, historical movement data already exist from a large-scale radio-telemetry study during the 1980's (Siniff and Ralls 1988). These data will allow a comparison not only of a population that is different temporally from the current sea otter population but, also one that was increasing at a rate of 5% per year.

Understanding how individuals in the current population use their habitat and comparing those animals to individuals and their habitat use from an earlier population could help in determining underlying causes of increased mortality currently limiting population recovery (Chapter 2, this report). The large-scale analysis of weekly, monthly, quarterly, and yearly movement patterns can be used to: a) improve upon the existing diffusion model of range expansion (Lubina and Levin 1988), b) parameterize population simulations that can be used for evaluating management options such as translocation and effect on fisheries, and c) understand spatial distribution using home range analysis to provide fundamental information about social organization. On the other hand, the small-scale analysis using individual based movement models to predict daily movement patterns can be used to evaluate effect of habitat complexity and variation (e.g. bathymetric complexity, bottom type, kelp canopy) on individual movements thus providing information about how sea otters use their habitat and which features of that habitat are most critical.

This study examines the temporal and spatial variation between past and current sea otter populations based on several criteria, including average length of movement over several time intervals, average turn angle on successive days, estimates of home range, and a correlated random walk (CRW) individual based movement model. These results will be used to suggest mechanisms for the emergent patterns of a mammalian carnivore from an ecological perspective and interpret the findings within the context of a mammalian movement model.

Background of Movement and Spatial Analyses

The analysis of animal movement

Studies of individual movement in animals have employed two methodologies. One is based on simulation models in which rules for movement are quantified and the computer is used to generate extended movement sequences based on observed movement patterns (Siniff and Jessen 1969, Jones 1977). This approach took hold in the 1970s with the advent of the personal computer (Jones 1977, Root and Kareiva 1984) and seemed to be a powerful approach for studying animal movement. However, these models are linked to the specific organism being studied; therefore, generalizations that are applicable to other species have been slow to emerge (Turchin 1998).

The second method utilizes analytical models that rely on the assumption of random motion and diffusion (Skellam 1951). Diffusion models and their application to ecological issues have a long history (Turchin 1998). Early uses in mathematical ecology included the study of random migration in species (Pearson and Blakeman 1906) as well as random dispersal in theoretical populations (Skellam 1951). In the 1980s, diffusion models were used for such ecological issues as predicting range expansion in sea otters (Lubina and Levin 1988). One major drawback to the general diffusion models, however, is that assumptions of animal movement are oversimplified for the purpose of the model, and thus often do a poor job of describing movement of real organisms. Diffusion models seem to be a better fit when used to explain the movement of populations (Marsh and Jones 1988).

An alternative solution to the limitations of simulation modeling as well as the general diffusion approach comes in the form of random walk models. Several random walk models were reviewed by Marsh (1988) and revisited by Turchin (1998). In the most basic random walk model (an uncorrelated random walk), step length and direction of movement are independent of one another, and an animal will either choose a direction based on the surrounding environment or the previous move. This model relies on very simplified assumptions of animal movement such as one-dimensional space, fixed move lengths, no correlations between moves, and that organisms' move independently of each other.

A second type of random walk model explicitly takes into account correlations between move lengths and direction and so is appropriately referred to as a correlated random walk (CRW). Kareiva (1983) developed a CRW model that utilizes the two movement parameters: step or move length, and turn angles. This process allows a summary of behavior called net squared displacement (Rn^2) that enables comparisons to be made between different organisms, or for the same organism in different situations. Rn^2 is a better indicator of how a species uses a two-dimensional area as opposed to simple net displacement (Rn) which only gives a one-dimensional idea of how an animal moves in a linear way.

Since the mid-1980s theoreticians have used one-, two-, and three-dimensional CRW models to simulate an animal's movement. However, there have been few empirical tests of these models and those that do exist have mostly been performed on insects (Kareiva and Shigesada 1983)) and ungulates (Bergman *et al.* 2000). Quantitative work to describe how carnivores move at large temporal scales and how individual movement in particular affects population level processes is generally lacking (Siniff and Jessen 1969, Ford and Krumme 1979, Kareiva and Shigesada 1983, Lubina and Levin 1988, Marsh and Jones 1988, Bergman et al. 2000).

Home Range Estimation

Since home range was first defined by Burt (1943) as "an area used by the individual in its normal activities of foraging, mating, and caring for young," radio-telemetry locations have been used to quantify home ranges (Kernohan *et al.* 2001). However, White (1990) pointed out that the previous definition of home range had two problems: a) the use of the word normal and, b) the lack of temporal component.

As a result, White (1990) gave a more probabilistic definition of home range when he defined a home range as "the probability of finding an animal at a particular location. The distribution of an animal's position in a plane was coined as "utilization distribution" by several scientists (Jenrich and Turner 1969, Ford and Krumme 1979, Anderson 1982). Kernohan (2001) further defined a home range based on the utilization distribution as "the extent of area with a defined probability of occurrence of an animal during a specific time period." The idea of "center of activity" in home ranges, introduced by Hayne (1949), is often used in conjunction with utilization distributions. Intrinsic to both these ideas is that an ecological understanding of an animal's home range must comprise some information about the level of use in various parts of the home range (Kernohan *et al.* 2001).

Based on these definitions and others, a variety of methods have been used to calculate home range. The various quantitative techniques have been reviewed by Kenward (1987) and White (1990), and contrasted and compared by Worton (1987, 1989, 1995), Boulanger (1990), Seaman (1996,1999). Quantitative methods of calculating home ranges fall into three categories: 1) polygon methods, 2) grid cell methods, and 3) probabilistic methods (Kernohan *et al.* 2001). Minimum convex polygon is the oldest and most commonly used home range estimator (Seaman *et al.* 1999) and simply connects outer locations of a series of points to form a convex polygon. The grid cell method (Siniff and Tester 1965) uses a set grid. This is laid over a set of location points and allows for two-dimensional contouring of ranges but does not calculate home range area as effectively as probabilistic methods (Harris *et al.* 1990). Probabilistic methods that contour around different intensities of use can result in smooth outer boundaries and multiple centers of activity (Kernohan *et al.* 2001). These probabilistic methods try to determine an animal's utilization distribution by assuming a particular probability distribution or by attempting to characterize a variety of distributions (e.g. harmonic mean and kernel) (Harris *et al.* 1990).

Past analyses of habitat use by sea otters have used minimum convex polygon methods to quantify home range sizes (Garshelis and Garshelis 1984, Jameson 1989, Ralls *et al.* 1996b). However, there are several inherent problems with polygon analysis including: 1) no measure of internal space usage, 2) sample size autocorrelation (particularly with small samples), and 3) sensitivity to outliers (Worton 1987). More recently, kernel density estimators have been used for home range analyses. These show great promise (Gubbins 2002, Heide-Jorgensen *et al.* 2003). Attractive features of kernel home range estimators include: 1) less sensitivity to sample size (stabilizing with > 50 locations), 2) less sensitivity to auto-correlated data, 3) calculation of home range boundaries based on the entire utilization distribution, 4) non-parametric assumptions (i.e., they do not violate assumptions of known distributions), 5) calculation of multiple centers of activity, and 6) less sensitivity to outliers (Kernohan *et al.* 2001).

Methods

Data Collection

Sixty-six southern sea otters were caught between March 2001 and May 2003 in two locations (Cambria and Point Conception) along the central coast of California (Figure 13). Each individual was equipped with abdominally implanted VHF radio transmitters (Advanced Telemetry Systems, Inc., MN), time-depth recorders (Mark VII TDRs – Wildlife Computers, Inc., WA) and color-coded flipper tags. Fifty-eight animals were also caught between October 2000 and October 2003 off the coast of Monterey (Figure 13), and implanted and tagged with the same instrumentation listed previously, in a cooperative study with the Western Ecological Research Center (WERC) of the United States Geological Survey (USGS), the Alaska Science Center of the USGS, and the Monterey Bay Aquarium., In addition to these two study groups, data also exist from forty animals that were captured in a previous study conducted between March 1984 and December 1985 in the following five locations: the Monterey Peninsula, Point Sur, Lopez Point, Point Piedras Blancas, and Morro Bay (Siniff and Ralls 1988) (Figure 14).

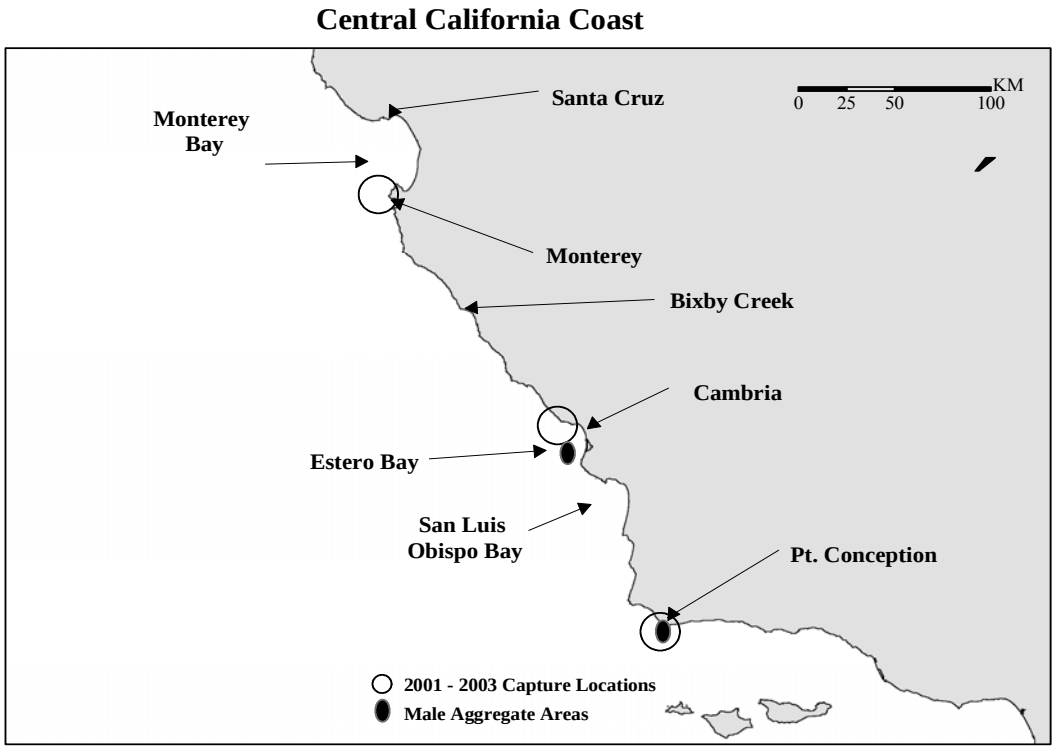

Figure 13. Capture locations for sea otters for the current Cambria sub-population and the current Monterey sub-population.

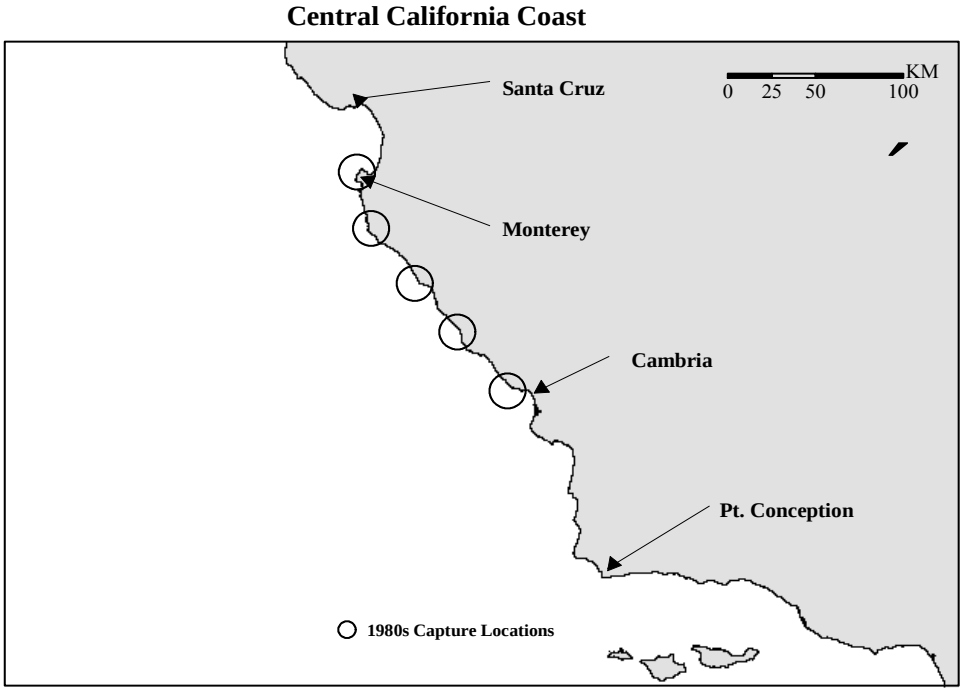

Figure 14. Capture locations for the 1980s sea otter population study (Siniff and Ralls 1988).

Locations of individual sea otters were determined from signal direction of animals using VHF radio receivers (Communication Specialists, Inc. Model R1000) and a handheld directional 3– element Yagi antenna. After a radio signal was received, that animal's location was determined by visual observation of the otter or triangulation on the VHF signal (White and Garrott 1990). If possible, a visual sighting of the animal was acquired using either high powered binoculars (Eagle Optics Ranger 10x50) or by field telescope (Questar Field Model 50x), and a bearing to the animal's location was recorded using a Silva Ranger compass. After the bearing was noted a laser rangefinder (Bushnell Yardage Pro 1000) was used to determine the distance between the otter and the observer. These parameters were used to estimated a coordinate or "fix" for the animal using global positioning system (GPS) technology (Garmin Map 76 GPS). Location data were collected using Universal Transverse Mercator Grid System (UTMs) and recorded in handheld organizers (Palm Pilot M500). Resights of each animal were collected daily, if possible. Comparable methods of data collection were used in the 1980s study (Siniff and Ralls 1988).

Both the current study and the 1980s study used VHF radio receivers to determine signal direction. Siniff and Ralls (1988) used a directional 4 – element Yagi antenna mounted on the roof of a vehicle as opposed to the current 3 – element hand held antenna. When individuals could not be located for several days in a row Siniff and Ralls (1988) also used aircraft mounted VHF radio equipment to search for individuals. When an animal's signal was located Siniff and Ralls (1988) used the same two methods for estimating position as the current study; visual observation and radio triangulation. However, Siniff and Ralls (1988) also used a third method when neither of the first two was possible. This method entailed allowing a location to be recorded based on the best judgment of the observer using direction and strength of radio signals.

Siniff and Ralls (1988) collected daily resights of the tagged and instrumented sea otters in three primary locations: Monterey, Big Sur, and Pt. Piedras Blancas. Daily resights of animals from the current Piedras Blancas – Point Conception Study (Cambria) were collected in the most part between Pt. Piedras Blancas to Avilla Beach, CA (Figure 15). Daily resights of animals from the current Monterey Bay Study (Monterey) were collected from Del Monte Beach in Monterey, CA to Point Lobos south of Carmel, CA (Figure 16). Searches for missing otters were undertaken from a fixed-wing aircraft equipped with radio receivers and/or small boats. The location of an individual was recorded for each resight, along with presence or absence of a pup, and any unusual activity.

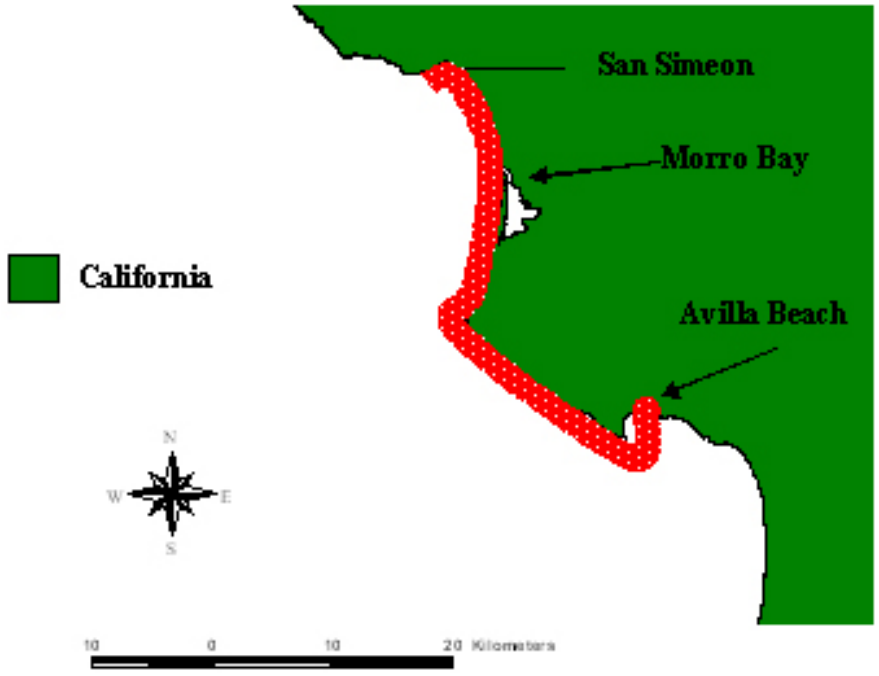

Figure 15. Main resight area of sea otters in the current Cambria sub-population.

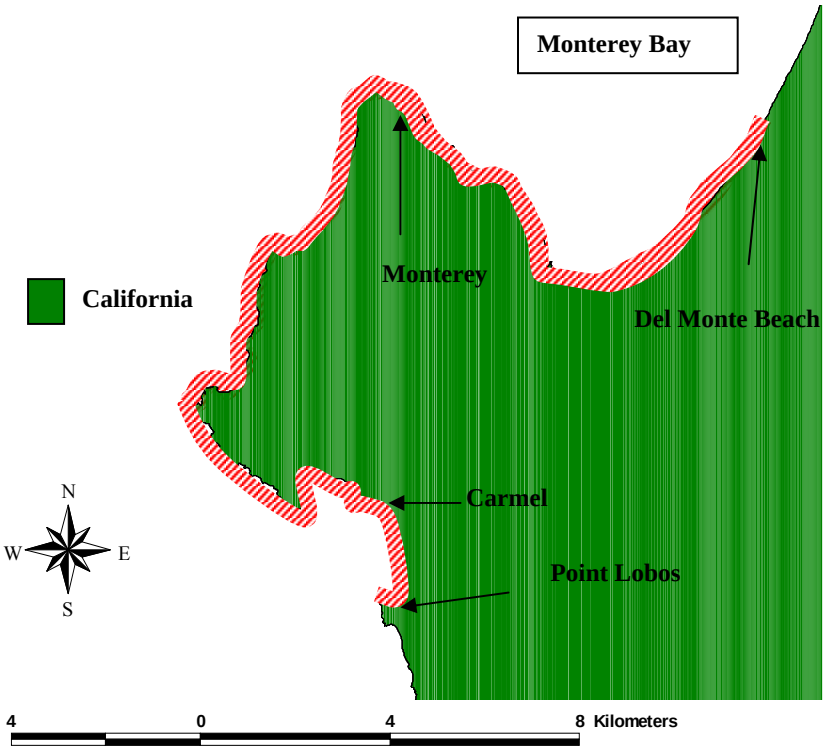

Figure 16. Main resight area of sea otters in the current Monterey Bay sub-population.

Animals from both current studies (Cambria and Monterey) as well as the 1980s study were divided into four age/sex-classes. Individuals under three years old that were independent of their mother were categorized as sub-adult females or males. Individuals that were older than three year of age were categorized as adult females or males.

Data Analysis

Sea otter home ranges were calculated using Arc View 3.2 Animal Movement Extension. Four methods were used: minimum convex polygon (MCP), adaptive kernel (AK), adjusted kernel (ADJK), and Calculated Area of Use (CAU). MCP and AK were calculated by fixed methods in Arc View 3.2. However, ADJK home range was calculated using an analysis mask in Arc View 3.2 to exclude the terrestrial environment as well as any area outside the 40m bathymetry line which is typically considered unsuitable habitat for sea otters (Laidre *et al.* 2001). CAU home range was determined as the product of the linear distance between kernel edges and the perpendicular distance to the shore in which 95% of all data points lay. A home range area was calculated for each individual using a minimum of 50 days of locations spaced out over one year from that individual's data set (Millspaugh and Marzluff 2001). If an animal did not have a minimum of 50 days of locations it was excluded from the analysis.

To calculate the mean and variance of daily, weekly, monthly, quarterly, and yearly move lengths for each individual for each time period, all location points collected over the entire study for that individual were used to determine two things: 1) the best location point for each day in the case of multiple resights (only visual resights within 1000 meters of shore were used) and, 2) whether the points occurred on consecutive days. A daily move length was calculated whenever two location points from consecutive days were available. Each animal was required to have a minimum of 50 daily move lengths. Once it was determined that the animal met the minimum requirements, the location points from the consecutive days were sampled with replacement 100 times to determine a mean daily move length for that individual. Sampling with replacement was done in order to standardize the analysis so that individuals with as few as 50 daily move lengths could be compared with individuals with as many as 300 daily move lengths.

A weekly move length for the same individual was calculated using two points that occurred within 6-10 days of each other. Each animal was required to have a minimum number of 25 weekly move lengths. Once again, if the animal's data met the minimum criteria, the location points were sampled with replacement 50 times to calculate the mean weekly move length for that individual. This process was repeated for the same individual to calculate mean monthly, quarterly, and yearly move lengths using similar criteria. A mean monthly move length was calculated using two points that occurred within 28 – 35 days of each other. Each animal had to have a minimum of 12 monthly move lengths. The monthly locations were sampled with replacement 25 times to calculate the mean monthly move length for that individual. A mean quarterly move length was calculated using two points that occurred within 85 – 95 days of each other. Each animal had to have a minimum of six quarterly move lengths. The quarterly locations were sampled with replacement 25 times to calculate the mean quarterly move length for that individual. A mean yearly move length was calculated using two points that occurred within 340 – 380 days of each other. Each

animal had to have a minimum of one yearly move lengths. The yearly locations were sampled with replacement 10 times to calculate mean yearly move length for that particular individual. A mean move length for every time period (day, week, month, quarter, and year) was calculated for each individual animal if their data met the minimum criteria.

Two movement parameters for each animal were calculated to determine the appropriateness of a CRW model: 1) mean daily move length over five consecutive days, and 2) mean turn angle for the same five consecutive days. Each individual was required to have a minimum of 20 of these five consecutive day periods of movement. The five consecutive days time period was chosen because it was the longest period of consecutive days of locations that was collected for many individuals and therefore it allowed the inclusion of the greatest number of animals from each study for comparison. Mean daily move length and turning angle was calculated for each individual by sampling with replacement 100 times from that individual's five consecutive day periods.

Turning angles for each individual were then analyzed by classifying each successive angle as "left" or "right" and using Chi-Square analysis to determine whether there was equal probability of the animal turning left or right (Turchin 1998). This was calculated in order to establish if angles were symmetrical. Determination of the symmetrical or non-symmetrical distribution of turn angles around 0° established which CRW function to use. The five day expected net squared displacement ($E(Rn^2)$) for each individual was calculated using the two movement parameters described above in Kareiva (1983) formula:

$$\mathbf{E(Rn^2) = nm_2 + 2m_1^2 (y/1- y) (n – (1- y^n / (1 - y))}$$

Where: Rn^2 = net squared displacement
n = number of consecutive moves
m_1 = mean move length
m_2 = mean squared move length
y = average cosine of turning angle

Observed net squared displacement $O(Rn^2)$ for each individual that met the minimum criteria listed above was calculated at the same time as $E(RN^2)$ using the same five consecutive day sets. To calculate $O(Rn^2)$ for day one, 100 day ones were chosen, for each day the squared displacement was calculated, and from this the mean observed squared displacement for all day ones was calculated. The process was repeated for days 2-5 to determine the mean observed squared displacement for each successive day. The $O(Rn^2)$ for each day was compared to the $E(Rn^2)$ for each day. MATLAB 6.5.0 was used to calculate all parameters.

Statistical Analysis

SYSTAT 10 software was used for the following statistical analysis. Variation among individuals, age/sex classes, and study for all move lengths (daily, weekly, monthly, quarterly, and yearly) as well as variation in turning angles were analyzed using Kruskal-Wallis homogeneity of variance test. A single factor ANOVA (factor: time) was used to test for significant differences in movement over time for all three populations. A two-factor

ANOVA (factors: study and age/sex class) was used to test for significant differences in the following: 1) spatial variation in daily, monthly, weekly, quarterly, and yearly move length averages for class and study, 2) temporal variation in daily, monthly, weekly, quarterly, and yearly move length averages for class and study.

Paired t-tests were used to test for differences between the following: 1) MCP home range - AK home range, 2) AK home range - ADJK home range, and 3) ADJK home range - CAU home range. A two factor ANOVA (factors: study and age/sex classes) was used to determine differences in 1) spatial variation in the current population using two methods of home range calculation (ADJK and CAU), and 2) temporal variation between past and present populations using two methods of home range calculation (ADJK and CAU). Bonferoni post-hoc testing was used to quantify variation in age/sex classes for the same two methods of home range calculation. The experiment wide Type I error rate (α) was set to 0.05 for all statistical analysis.

To provide a measure of the variance around the E (Rn^2), MATLAB 6.0.5 was used to bootstrap 5,000 pseudo-paths for each animal using the known distribution of move lengths and turning angles. For each simulation an animal was started at an arbitrary location (drawn from the empirical data) and given a random initial direction. Next, a move length was randomly drawn from the empirical distribution and a new location determined based on the move length and initial random direction. Next a turning angle was randomly drawn from the empirical distribution of turning angles along with another move length and from this the next location was determined. This procedure was reiterated five more times; after the fifth step, E (Rn^2) was calculated based on how far the animal had come from the first arbitrary location. The smallest and largest 2.5% of the calculated E (Rn^2) values from the 5,000 simulations were discarded and the extremes of the remaining values were used as the 95% confidence intervals (Turchin 1998).

Results

Move Lengths

Average move length variances did not differ for any time period (Table 2). Move lengths across all time frames, for all studies, and for all individuals were log normally distributed. Measured individual move lengths ranged from 0.2 – 490 km depending largely on the time scale (*i.e.* days to years) (Appendix E). Most individuals moved increasing distances over greater time periods (Appendix E). There was also wide variation for move lengths across age/sex classes, study areas, and time periods (Table 3). For instance, move lengths within age/sex classes ranged from 0.12 - 72 km for adult females, 0.15 – 401 km for adult males, 0.26 – 111 km for sub-adult females, and 0.35 – 490 km for sub-adult males. Overall, for individuals, analysis of variance indicated that move length increased significantly with increased time period, up to one quarter of a year ($F_{df\,2} = 90.76$, $p < 0.0001$). No increase in move lengths was detected at time intervals beyond one quarter year (Figure 17).

Table 2. Kruskal – Wallis homogeneity of variance results for average move lengths over five time periods. Data is pooled from all studies, 1980s, current Cambria, and Monterey Bay.

Time	K-W stat	p
Day	125	0.46
Week	119	0.49
Month	112	0.42
Quarter	133	0.38
Year	124	0.47

Table 3. Average move lengths (meters) over five time periods for three studies; 1980s, Cambria, and Monterey Bay, and for four age- and sex- classes; adult female (AF), adult male (AM), sub-adult female (SF), and sub-adult male (SM).

Study	Class	Day	Week	Month	Quarter	Year
Ca1	AF	583	2276	3136	5533	12309
Ca2	AF	500	1776	2654	4487	3853
MBA	AF	396	938	2111	3585	4140
Ca1	AM	310	1045	2357	3651	8282
Ca2	AM	336	2381	10835	43536	53306
MBA	AM	279	485	1396	7341	3862
Ca1	SF	744	2562	5260	8614	21435
Ca2	SF	303	526	711	1006	1550
MBA	SF	470	788	1485	1436	20578
Ca1	SM	1512	2253	7155	11451	11633
Ca2	SM	*	*	*	14192	39542
MBA	SM	253	296	649	6557	24516

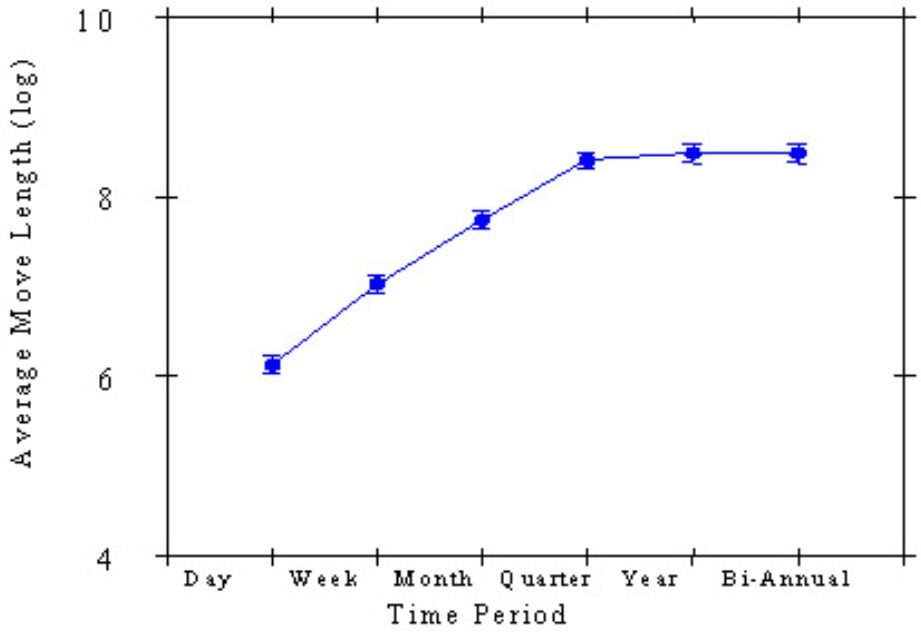

Figure 17. Mean move length (log) using pooled data from the 1980s population, the current Cambria sub-population, and the current Monterey Bay sub-population over six time periods.

Taken across all age and sex classes, daily move lengths for the current study did not differ significantly between study areas. Individuals in the Monterey area moved anywhere from 0.13 – 0.93 km per day while those in the Cambria area moved between 0.15 – 1.15 km per day. In contrast, overall movements differed between study areas for all other time periods (Table 4). At longer time periods, movement was consistently greater for the animals in the Cambria area. Move lengths also differed significantly between age and sex classes for all time periods (Table 4). Females move longer distances on a daily basis (Table 3). Males, on the other hand moved significantly more than females at all time periods greater than a day. Age/sex class differences interacted significantly with study area when evaluated on the time scales of weeks, months, quarters, and years (Table 4). Cambria males moved longer distances than those in Monterey. Cambria adult females moved more than the Monterey females. However, Cambria sub-adult females move less than their Monterey counterparts.

Table 4. Analysis of variance results for spatial variation of average move length between two current sub-populations of sea otters (Cambria and Monterey Bay (MBA)) for five time periods and two factors; study, class and the interaction between study and class.

Time	Comparison	Factors	N	F	p
Day	Cambria - MBA	Study	97	0.55367	0.45
Day	Cambria - MBA	Age-Sex	97	14.337	<0.0001
Day	Cambria - MBA	Interaction	97	1.9163	0.13
Week	Cambria - MBA	Study	88	3.80833	0.05
Week	Cambria - MBA	Age-Sex	88	8.09111	<0.0001
Week	Cambria - MBA	Interaction	88	3.39545	0.02
Month	Cambria - MBA	Study	81	11.0701	0.001
Month	Cambria - MBA	Age-Sex	81	2.63914	0.05
Month	Cambria - MBA	Interaction	81	9.06211	<0.0001
Quarter	Cambria - MBA	Study	104	5.61151	0.02
Quarter	Cambria - MBA	Age-Sex	104	8.84053	<0.0001
Quarter	Cambria - MBA	Interaction	104	4.64114	<0.001
Year	Cambria - MBA	Study	98	4.53133	0.04
Year	Cambria - MBA	Age-Sex	98	7.7432	<0.001
Year	Cambria - MBA	Interaction	98	4.3585	0.01

Overall, individual move lengths for any time period did not differ significantly between the 1980s study and the Cambria study (Table 5). However, more complex time-related patterns were evident in the movement data as there were significant temporal interactions between age/sex classes and study for all time periods (Table 5). For instance, males moved longer distances in the current Cambria study (0.18 - 490 km) than they did in the 1980s (0.21 – 111 km). Females, in contrast, had longer overall move lengths during the 1980s (0.02 km – 22 km) than they did during the current Cambria study (0.26 km – 15 km). Even though

significant time-related differences were detected for particular age/sex classes because of the significant interaction it was difficult to interpret those differences.

Table 5. Analysis of variance results for temporal variation of average move length between the current population in Cambria and 1980s population for five time periods and two factors; study and class, and the interaction between study and class.

Time	Comparison	Factors	N	F	p
Day	1980s - Cambria	Study	79	0.91	0.34
Day	1980s - Cambria	Age-Sex	79	1.61	0.12
Day	1980s - Cambria	Interaction	79	5.69	0.001
Week	1980s - Cambria	Study	73	0.4	0.52
Week	1980s - Cambria	Age-Sex	73	1.78	0.14
Week	1980s - Cambria	Interaction	73	3.01	0.03
Month	1980s - Cambria	Study	76	0	0.99
Month	1980s - Cambria	Age-Sex	76	4.28	0.007
Month	1980s - Cambria	Interaction	76	3.97	0.01
Quarter	1980s - Cambria	Study	92	0.52	0.47
Quarter	1980s - Cambria	Age-Sex	92	7.01	<0.0003
Quarter	1980s - Cambria	Interaction	92	3.71	0.014
Year	1980s - Cambria	Study	83	0.49	0.48
Year	1980s - Cambria	Age-Sex	83	5.44	0.001
Year	1980s - Cambria	Interaction	83	7.6	<0.0001

Home Range

Sea otter home ranges varied from 1.0 – 2497 km^2, depending on class, study, and methodology (Appendix F). Overall, for all studies, minimum convex polygon (MCP) provided the largest home range estimates (47 – 852 km^2), followed by adaptive kernel (AK) (21 – 704 km^2), adjusted adaptive kernel (ADJK) (14 – 390 km^2), and calculated area of use (CAU) (8 – 139 km^2). However, there were various apparent inconsistencies across these different methodologies with regard to the patterns of variation among classes, between study periods, and between specific areas.

For all studies sub-adult males had the largest home range areas, followed by adult males, sub-adult females, and adult females. This ranking was consistent for all four methods of home range calculation (Table 6). However, the extent to which home range sizes were seen to vary among particular age/sex classes differed somewhat depending upon method. For

instance, the MCP method indicated significant differences between sexes (*i.e.* males had larger home range areas than females) but not between age classes within sexes (*i.e.* there were no differences in adults and sub-adults) (Table 7). The other three methods, in contrast, showed that the home ranges of sub-adult males were significantly greater than those for all other age/sex classes (Table 6). The AK, ADJK, and CAU methods provided little evidence of variation in home range sizes between adult and sub-adult females. However, these same methods provided estimates of adult male home ranges that were significantly larger than those of adult females (Table 8).

Table 6. Average home range area (km^2) using four methods; minimum convex polygon (MCP), adaptive kernel (AK), adjusted kernel (ADJK), and calculated area of use (CAU). Two parameters used to calculate CAU are linear shoreline used (LIN USE) and area used perpendicular to shoreline 95% of time (OFF). Calculations were made for four age – and sex – classes, adult female (AF), adult male (AM), sub-adult female (SF), and sub-adult male (SM).

Class	MCP	AK	ADJK	CAU	LIN USE	OFF
AF	47	21	14	8	9	0.8
AM	420	211	105	19	15	1.0
SF	123	67	42	15	12	1.1
SM	352	704	390	139	54	2.5

Table 7. Bonferoni post-hoc pair wise comparisons for four age – and sex – classes, adult female (AF), adult male (AM), sub-adult female (SF), and sub-adult male (SM), using four methods of home range calculation, minimum convex polygon (MCP), adaptive kernel (AK), adjusted kernel (ADJK), and calculated area of use (CAU).

		p	p	p	p
Method	Class	AF	AM	SF	SM
MCP	AF	1.00			
MCP	AM	<0.001	1.00		
MCP	SF	1.00	0.02	1.00	
MCP	SM	<0.0001	0.77	0.002	1.00
AK	AF	1.00			
AK	AM	0.01	1.00		
AK	SF	1.00	0.26	1.00	
AK	SM	<0.0001	0.01	<0.001	1.00
ADJK	AF	1.00			
ADJK	AM	0.01	1.00		
ADJK	SF	1.00	0.35	1.00	
ADJK	SM	0.0001	0.002	<0.0001	1.00
CAU	AF	1.00			
CAU	AM	0.68	1.00		
CAU	SF	1.00	1.00	1.00	
CAU	SM	<0.0001	<0.0001	<0.0001	1.00

Table 8. Average home range area (km^2) using four methods of home range calculation, minimum convex polygon (MCP), adaptive kernel (AK), adjusted kernel (ADJK), and calculated area of use (CAU), as well as two parameters, linear shoreline used (LIN USE) and perpendicular-distance of off shore use of 95% of all locations. Calculations are for three studies; 1980s, current Cambria, and current Monterey Bay (MBA), and for four age – and sex – classes, adult female (AF), adult male (AM), sub-adult female (SF), and sub-adult male (SM).

Study	Class	MCP	AK	ADJK	CAU	LIN USE	OFF
1980s	AF	70	35	21	13	13	0.9
Cambria	AF	52	29	19	11	10	1.0
MBA	AF	30	8	5	3	7	0.4
1980s	AM	478	293	148	31	21	1.1
Cambria	AM	811	387	191	31	26	1.1
MBA	AM	33	2	2	1	2	0.5
1980s	SF	216	121	74	25	18	1.3
Cambria	SF	15	5	5	4	4	1.0
MBA	SF	10	3	3	2	6	0.4
1980s	SM	1122	734	407	163	79	2.0
Cambria	SM	1353	1252	690	158	59	2.9
MBA	SM	3	3	2	4	4	1.0

For all four methods of home range analysis, sea otters from the current Cambria area had significantly larger home ranges than those from the current Monterey area (Figure 18). It is interesting to note that Cambria male core areas are extremely far apart and for the most part represent entirely separate home range areas (Figure 25). Monterey males sometimes have multiple core areas within one continuous home range. However, they typically have one home range and one core use area (Figure 26).

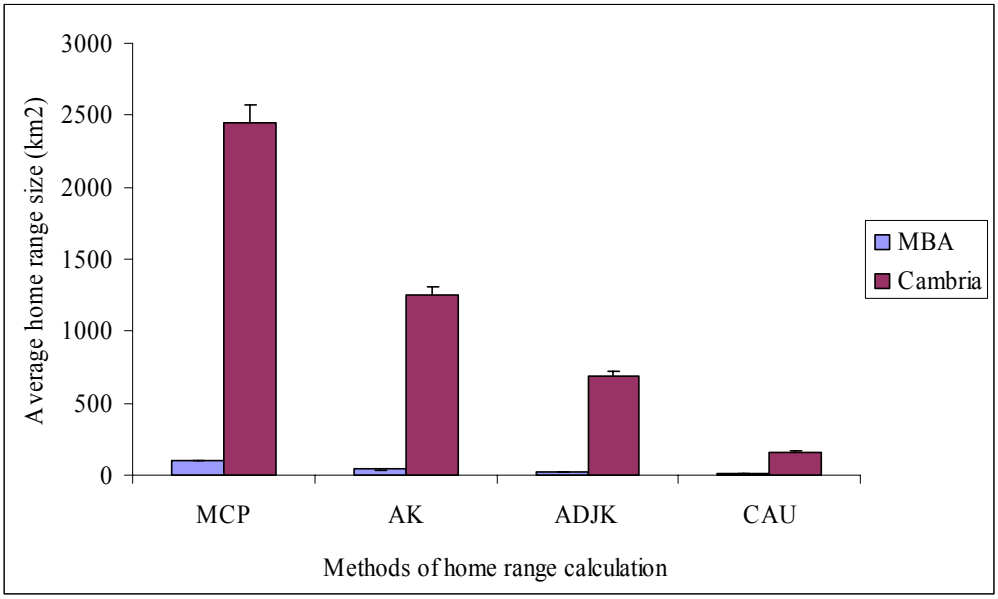

Figure 18. A spatial comparison between two current sub-populations, Monterey Bay (MBA) and Cambria, of four methods of home range analysis; minimum convex polygon (MCP), adaptive kernel (AK), adjusted kernel (ADJK), and calculated area of use (CAU) for pooled data from all age- and sex-classes.

The spatial differences contrast with the temporal differences found between the 1980s study and the current Cambria study. These studies home range areas differed only when using ADJK and CAU methods. When home range areas were calculated using ADJK and CAU methods, individuals from the 1980s study had significantly larger areas than did individuals from the current Cambria study (ADJK, $F_{1,2} = 12.76$, $p < 0.0001$; CAU, $F_{1,2} = 14.89$, $p < 0.0001$).

Correlated Random Walk

Overall, pooled data, from all studies and all individuals fit the expectations of the CRW model (Figure 19). The model slightly under predicted actual net displacement for days 2 – 5 but the results lie well within the 95% confidence intervals. When examined by study, data from the 1980s study (Figure 20) and the current Monterey study (Figure 21) conformed to the expectations of the CRW model much better for days 2-4 than did data from the current Cambria study (Figure 22).

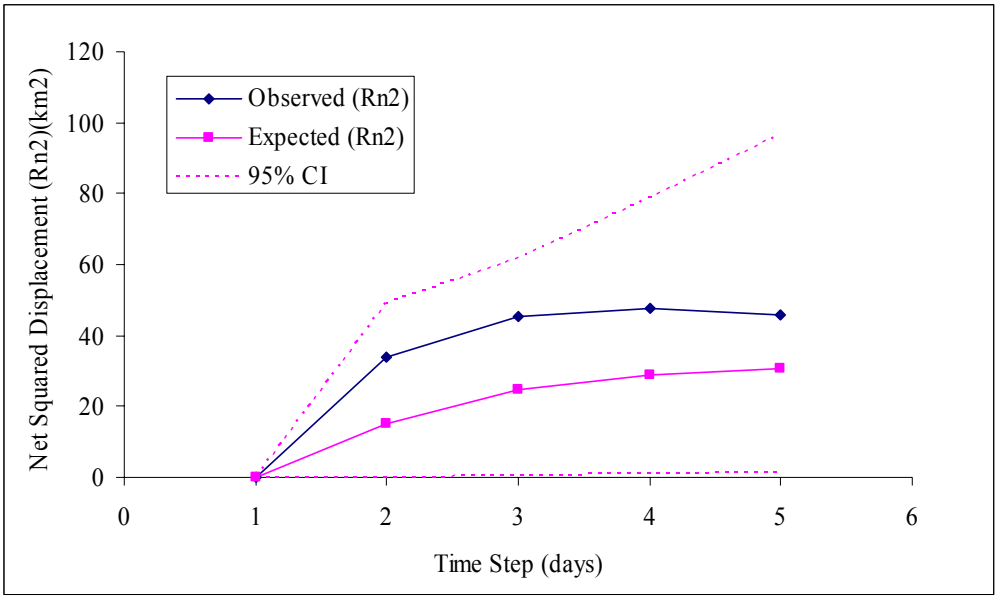

Figure 19. Average observed and expected net squared displacement (Rn^2) 95% confidence intervals of pooled data for three populations; 1980s, current Cambria, and current Monterey Bay.

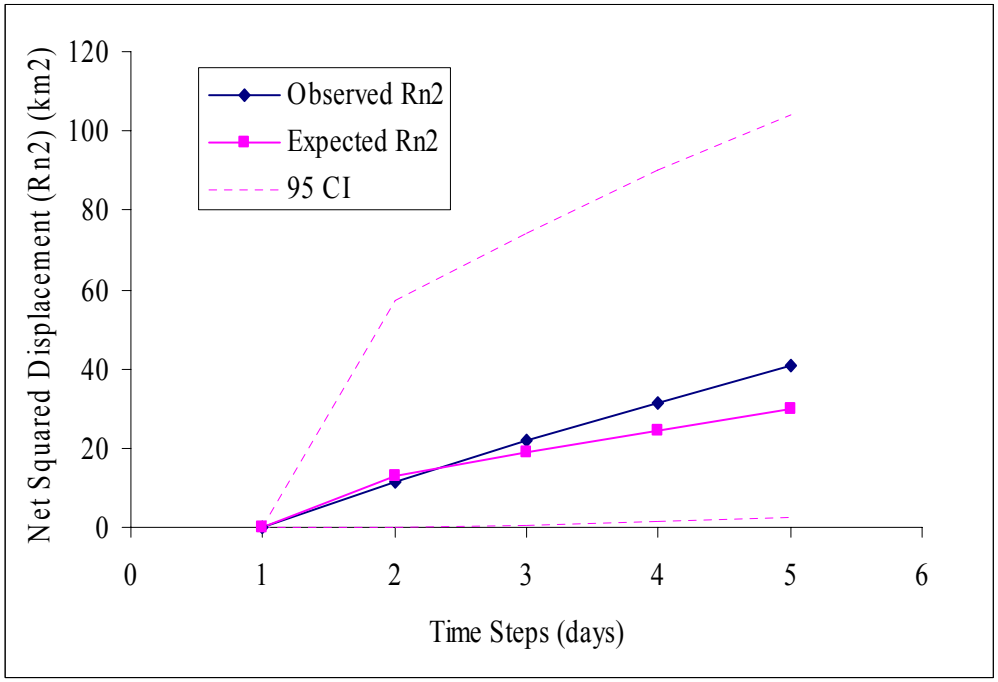

Figure 20. Average observed and expected net squared displacement (Rn^2) with 95% confidence intervals of 1980s population of sea otters for a five day time period.

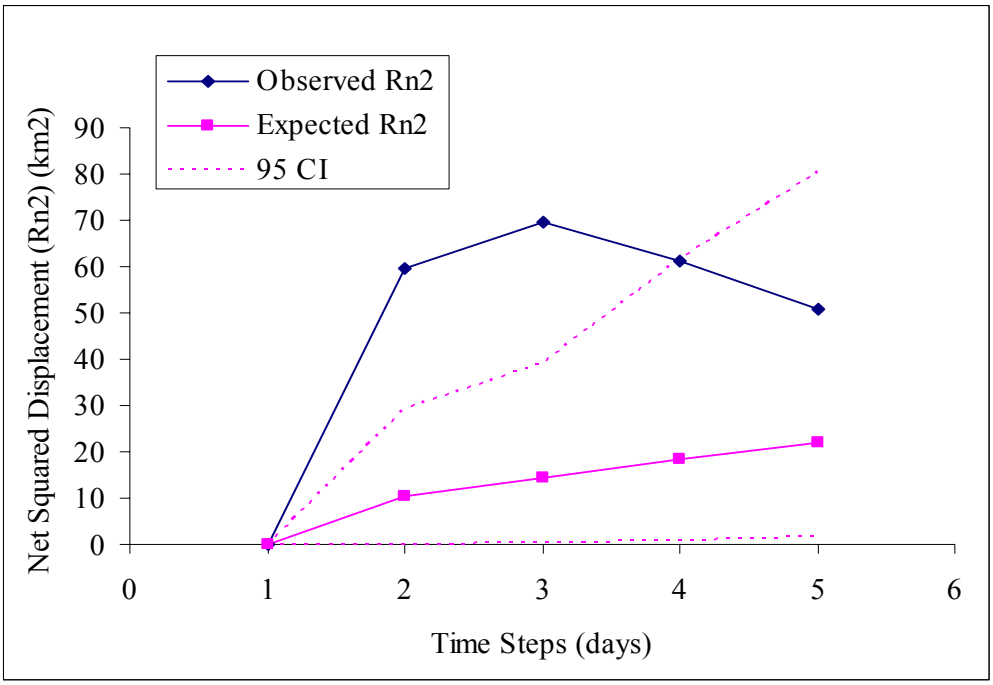

Figure 21. Average observed and expected net squared displacement (Rn^2) with 95% confidence intervals of current Monterey Bay sub-population of sea otters for a five day time period.

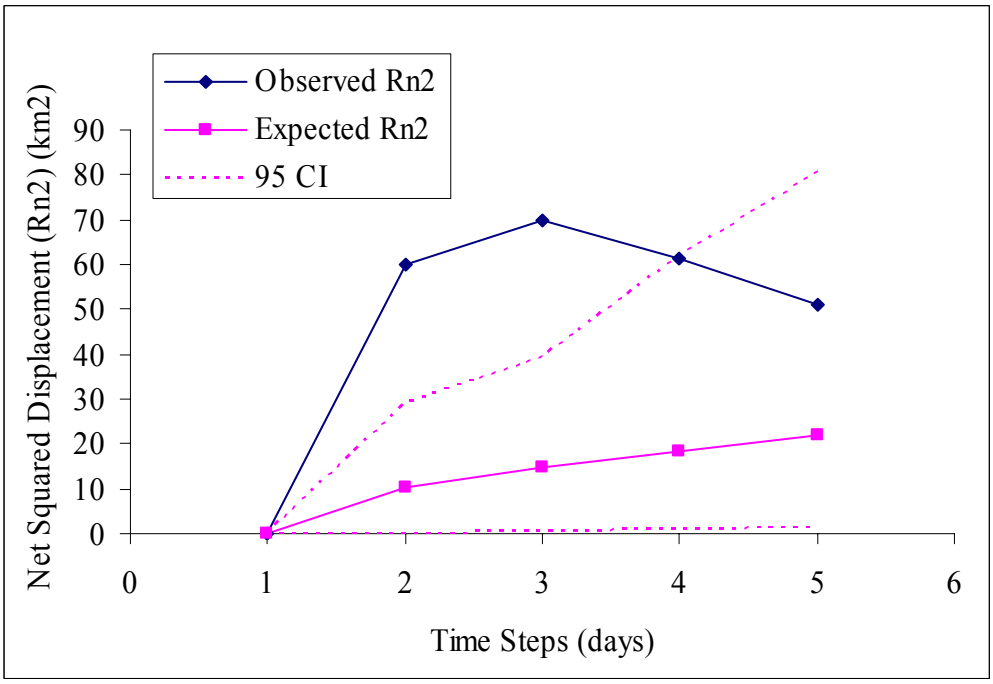

Figure 22. Average observed and expected net squared displacement (Rn^2) with 95% confidence intervals of current Cambria sub-population of sea otters for a five day time period.

Overall, data from the 1980s provide the best fit the expectations of the CRW model. For days 2–4, O (Rn^2) varied only slightly from E (Rn^2) (Figure 20). However, over a longer time period (by day 5) displacement for the 1980s animals seemed to be diverging in a linear fashion from that predicted by the model (Figure 20). The data from the current Monterey study indicated that E (Rn^2) was slightly less than O (Rn^2) for days 2 – 5 but overall, the O (Rn^2) are within the 95% confidence intervals (Figure 21). Data from the current Cambria population did not conform to the model expectations. This deviation seemed to be time related. For short time periods of < three days, there was a little evidence of model fitness but as the time interval was increased to 4 - 5 days, this lack of conformity disappeared and observed displacement moved within the expected displacement 95% confidence intervals (Figure 20).

Discussion

Understanding southern sea otter movement is important for a variety of reasons. The reinvasion or southern range expansion of the southern sea otter has created contentious issues between the species and various shellfisheries, and has placed the management of the sea otter by the U.S. Fish and Wildlife Service as a Threatened species squarely in the public eye. In light of recent range expansion around Point Conception (Figure 23) more active management, *i.e.* translocation of some members of the population, may become necessary. Other implications of the southern range expansion are worrisome as well. As sea otters move further south they come into closer proximity with offshore oil wells and shipping lanes. This is a major issue since it has long been noted that the southern sea otter is vulnerable to a catastrophic event such as an oil spill (Estes 1981, Ralls *et al.* 1992, Ralls *et al.* 1996a).

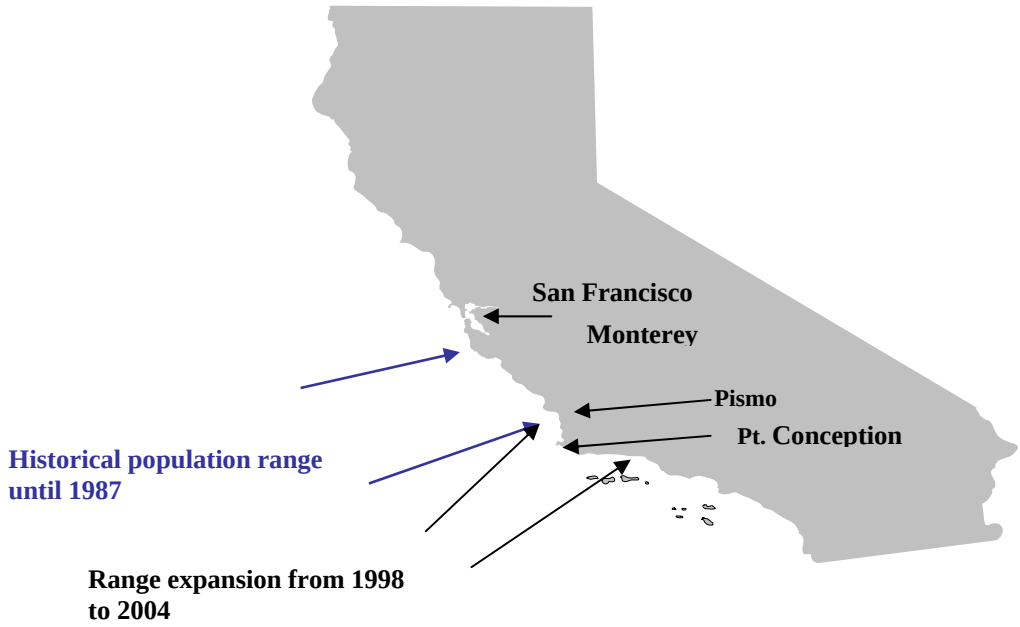

Figure 23. Historical range of the southern sea otter until 1987 and subsequent range expansion since 1987 – present around Pt. Conception, CA.

Also of concern is the potential resource limitation that may have been placed on the current population of southern sea otters throughout the central portion of the range as a result of increased sea otter density (Table 9). Time-activity budgets collected for the current population, both around the Monterey Peninsula and the Cambria area, indicate increased levels of foraging (foraging ~43% of a 24 hour period compared to foraging ~25% of a 24 hour period in the 1980s) which can be considered indicative of a resource limited population (Tinker 2004). Understanding how movement differs for a past population that was increasing and not food limited (Ralls and Siniff 1990), and for the current population where growth is unclear and there is probably resource limitation, could provide insight into how individual-based movement parameters change. As a result, this may give scientists a better idea into how differing parameters affect the ability of individual-based movement models to predict future range expansion and critical habitat needs for a threatened species.

Table 9. Average individual density/year of California sea otters for five areas of the central California coastline; Capitola Pier to the Monterey Breakwater (CP – MB), Monterey Breakwater to Point Lobos (MB – PL), Point Piedras Blancas to Cayucos Point (PPB – CP), Cayucos Point to Hazard Point (CP – HP), and Rocky Point to Point Conception (RP – PC).

Area	Habitat	1984 Density (otters/ km2)	1985 Density (otters/ km2)	1986 Density (otters/ km2)	1987 Density (otters/ km2)
CP - MB	Sandy	0.19	0.12	0.63	0.40
MB - PL	Rocky	1.83	2.32	2.56	3.04
PPB - CPT	Rocky	2.20	1.89	2.66	2.30
CPT - PB	Rocky	0.65	0.71	0.52	0.71
PA - PC	Mixed	0.00	0.00	0.04	0.02
Area	**Habitat**	**2001 Density (otters/ km2)**	**2002 Density (otters/ km2)**	**2003 Density (otters/ km2)**	**2004 Density (otters/ km2)**
CP - MB	Sandy	1.30	2.05	0.11	3.14
MB - PL	Rocky	3.32	2.60	3.20	3.04
PPB - CPT	Rocky	2.29	2.30	2.35	3.33
CPT - PB	Rocky	2.43	1.32	2.00	3.40
PA - PC	Mixed	0.63	0.82	1.08	1.02

Table 9. continued

Area	Habitat	Average 1984 - 1987 Density (otters/ km2)	Average 2001 - 2004 Density (otters/ km2)
CP - MB	Sandy	0.34	1.65
MB - PL	Rocky	2.44	3.04
PPB - CPT	Rocky	2.26	2.56
CPT - HP	Rocky	0.65	2.29
RP - PC	Mixed	0.02	0.89

Movement Patterns – Age- and Sex- Class Over Time

There was a great deal of variation in movement patterns of individuals in all age/sex classes. Sub-adult males moved more than other age/sex classes over a day and over a week. However, adult males moved greater distances over longer time periods (Table 3). Both sub-adult and adult males utilized most of the species range in California (Figure 23) which corresponds with a previous study (Ralls *et al.* 1992). On a daily basis, adult males moved the least of all age/sex classes. Biologically, this makes perfect sense. Adult males concentrate on several things during a day: defending a territory, mating, and procuring food. The size of a territory that a male can defend is based on a variety of factors including the health and age of the individual, available resources, and density of otters in the area. However, there is only so much time in a day and only so far an animal can patrol in order to defend its territory, therefore, average move lengths are constrained by territorial defense.

Alternatively, adult males are known to leave female areas during non-breeding seasons and aggregate into "male areas" which are typically along the range fronts (Garshelis and Garshelis 1984, Jameson 1989). Traveling to range edges constitutes a long distance movement on the part of males. By observing the adult males for periods of time longer than one day, it is more likely that these long distant movements will be detected. As a result, average move lengths will be greatly increased.

Sub-adult males move greater distances over a day and a week than all other classes (day – 1.5 km, week – 3.5 km) and are second only to adult males in average move length over longer time periods. These results are consistent with those of Jameson (1989) and Garshelis (1984) and support the idea that sub-adult males are forced to disperse from natal areas early in life, and that this dispersal process is almost continuously ongoing. This is typical behavior of polygynous mammals (Greenwood 1980). Sub-adult males are forced to avoid territorial male areas until they are at such a condition and age to challenge for their own territory. Densities have increased and the southern range front has expanded since the 1980s study. This expansion creates a situation in which a sub-adult male may have the need to move longer distances to avoid territorial males. Sub-adult males also travel to range

fronts like adult males but their movement was not as predictable as that of adult males. It was not evident that the young males were making multiple long distance moves over a year and then returning to areas of high female densities in order to establish territories. They do, however, appear to move among known aggregations of other males.

Adult and sub-adult females move more than males over shorter time periods (day and week). Females tend to use a longer linear amount of the coastline than adult males in their daily and weekly movements. Males are interested in two things within a home range: defense of the resources and utilization of those resources. Therefore males need to maximize space by incorporating the minimum amount of area they can defend but one that provides them with the necessary resources to survive. Obviously, female daily movements are not constrained by defending territories but are spent foraging, caring for young, and moving back into "female groups" to rest. Females therefore are more concerned with finding the best resources in an area and so seem to be moving longer distances on a daily basis.

Spatial Variation in Movement Patterns

Average daily move length of sea otters in the current study did not differ among locations. At all other time scales, animals in the central portion of the range (Cambria) moved longer distances than those in the Monterey area (Figure 24). The reason for these differences is uncertain. An examination of habitat type and current density estimates for these two areas showed that both areas consist of predominantly rocky substrate with moderate to large amounts of kelp (Laidre *et al.* 2001) and this type of habitat generally supports larger densities of sea otters than other substrate types (Riedman and Estes 1990). Densities of sea otters are also similar in these two areas (Table 9) (MB – PL and PPB – CPT). Because the two areas have similar habitats and density it seems unlikely that those two factors play a significant role in the move differences.

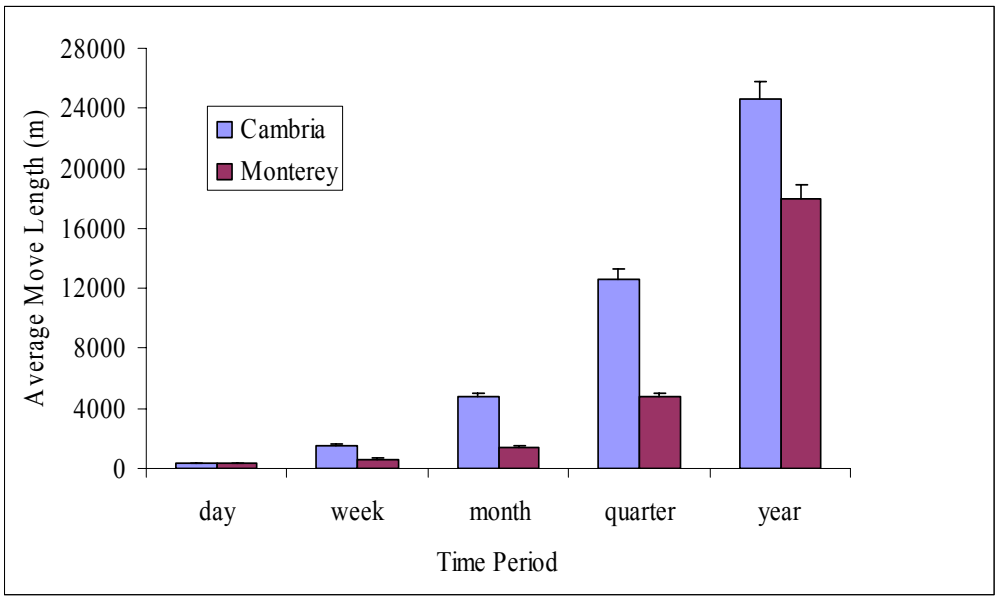

Figure 24. Spatial variation in move length for pooled age- and sex- class data from two current sub-populations (Cambria and Monterey Bay) over five time periods (day, week, month, quarter, and year).

Both the Monterey and Cambria animals are presumably food limited (Tinker 2004), however individuals in these two sub-populations are moving very differently over longer periods of time. The most obvious difference is that adult males from the Monterey population are not making long distance moves to the northern range front and are only occasionally moving to the central portion of the range, whereas the Cambria adult males are traveling to the southern range front several times a year. There are several reasons that may underlie the lack of long distance moves by the Monterey adult males. One reason lies with preliminary analysis of recent sampling of invertebrate prey species in Monterey and Cambria. These results have indicated that the Monterey Peninsula has greater species richness and abundance than does the Cambria intertidal area (Mark Carr, University of California Santa Cruz PISCO, pers. comm. 2004). Another reason for lack of long distance movement involves the geology of Monterey Bay. Monterey Bay is an entirely different habitat (soft and sandy sediment) from the rocky intertidal habitat of the Monterey peninsula and so the type, amount, and variety of prey changes dramatically. Sea otters are very individualistic foragers (Estes *et al.* 2003, Tinker 2004). Thus, individuals living in a rocky intertidal environment may find it difficult to venture into different habitats with different prey types until they are forced to do so by extreme densities and/or food limitation. In fact, range expansion has stalled at times when animals have reached areas of substrate changes both on the northern and southern end of the range (Lubina and Levin 1988). Another geologically important element is the presence of Monterey Canyon. Monterey Canyon plunges over one mile deep and formation of the canyon begins within a few hundred meters of the shore off the coast of Moss Landing in central Monterey Bay (Figure 13). Monterey Canyon plunges past the 40 meter bathymetry line less than a half kilometer off shore. Typically sea otters do not forage below depths of 40 meters and to determine critical sea otter habitat in the past the offshore boundary used has been the 40 meter isobath (Laidre et al. 2001). Because of these two geological characteristics, it is quite possible that Monterey Bay is functioning as an environmental barrier to northern movement for some sea otters residing around the northern end of the range.

Adult and sub-adult males from Cambria must also move through soft sediment habitats to reach the southern range front (Estero Bay, Shell Beach) (Figure 13). The sandy habitats in the north and south are roughly equivalent in size (Monterey Bay sandy habitat from shoreline to the 40 meter depth contour– 182.5 km^2; Shell Beach sandy habitat – 199.9 km^2). However, the central and southern males seem less constrained by these habitat differences as evidenced by multiple moves to male aggregate areas, and this is inconsistent with an 'environmental barrier" hypothesis.

Overall, adult males captured near Monterey weighed less and had smaller mass/length ratios than those captured near Cambria (Tinker 2004). However, even though the Monterey males were in poorer condition than the Cambria males they do not appear to move to the range edges where there is presumably no food limitation. The Cambria animals are also foraging in rocky habitat. As noted previously however, the Cambria area has less species richness and abundance with regard to specific sea otter prey items than does the Monterey Peninsula (Mark Carr, University of California Santa Cruz PISCO, pers. comm. 2004). As a result of prey composition differences the Cambria animals might need to move longer distances to find the required resources and hence be exposed to alternative habitats to the rocky intertidal. Being required to move longer distances in search of prey could have

provided the Cambria males with an advantage when it comes to venturing across long sandy bays. It seems evident that the central and southern males (Cambria) are employing a different strategy for survival than the Monterey males. As mentioned previously, Cambria male core areas are extremely far apart while Monterey males generally have one core use area within one home range. The Cambria males are establishing territories in areas of high female densities and during breeding seasons (Figure 25). At some point, they move south to aggregate in large "male groups" where food is plentiful and otter densities are much lower, resulting in non-continuous home range areas (Figure 25). When examining overall health and morphological characteristics between the two areas, central and southern males seem to have the edge at this time perhaps because of differing strategies. The strategy employed by the Cambria males seems to be paying off as the annual survivorship of the males caught in the central and southern portion of the range is significantly higher than all other classes examined in the current population (Tinker 2004).

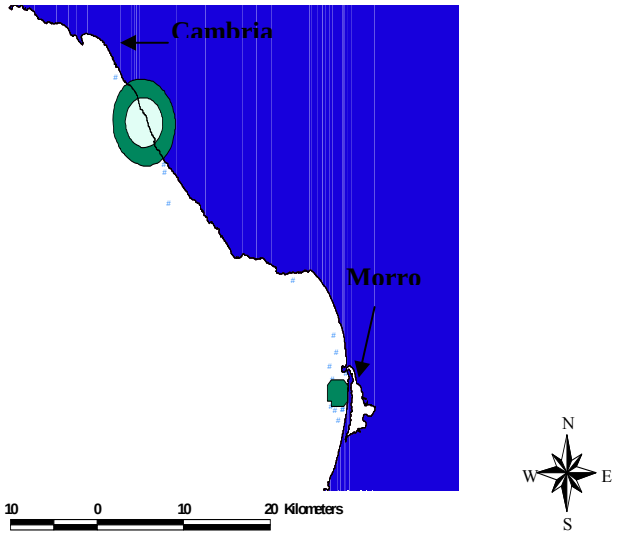

Figure 25. Typical multiple home range and core use area based on daily location data for male 6-183, from the current Cambria sub-population using adaptive kernel method of home range calculation. 95% probability area equals 48.5 km^2.

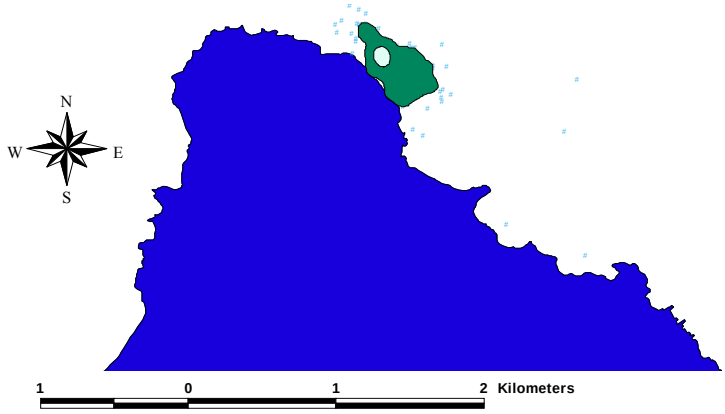

Figure 26. Typical single home range and core use area for male 4-204 from the current Monterey Bay sub-population using adaptive kernel method of home range calculation. 95% probability area equals 17.6 km^2.

Temporal Changes in Movement Patterns

The behavior of the Cambria study males are consistent with Jameson's findings (1989) that documented long-distance seasonal movements, but are also consistent with the intermediate movement findings of (Ralls *et al.* 1996b). Cambria males exhibited seasonal movements at the end of the winter months to male areas at the southern end of the range. However, they were not constrained by these long distance, end of winter movements as they also showed an intermediate movement pattern during other seasons. When males did leave their territory they typically traveled to areas of male aggregates found in several locations, including Morro Bay and Point Conception (Figure 13). Males captured as part of the central and southern range study at Point Conception also moved back north to many different locations, ranging from Avila Beach to Monterey, to establish territories for part of the year. Adult and sub-adult males in the 1980s also made long distance moves to the southern range front. However, 1980s males had a shorter distance to travel to reach the southern range front which occurred around Pismo Beach (Figure 23) than do the current males. Overall, the pattern suggests that the multiple long distance moves by the Cambria males are what is likely driving the temporal differences in average move lengths between the two populations.

Home Range – Age- and Sex- Class

Since males moved longer distances over a year than females, one might expect them to have the largest home range areas. Indeed, males did have larger home ranges than females. These results are highly influenced by the long distances that males move. Because MCP home range calculation is a method that connects the outer points of an animal's locations, long distance movements that might be considered outliers in other home range methods carry as much weight as any other point and greatly influence the size of the polygon. Since males tend to make long distance moves, this factor would significantly influence the size of the home range area and would logically result in home ranges that were much larger than those of females.

Adult males also had longer yearly move lengths than sub-adult males and so one would suspect that the home range areas of the adult males would be larger than sub-adult male home ranges. This was the case when using the MCP method. However, sub-adult males had larger home range areas when using the other three methods of home range calculation (AK, ADJK, and CAU) (Table 6) and this was slightly confounding. However, when considering how animals use their home ranges and how adult males typically defend territories for at least a portion of the year, the results are more reasonable. Many of the adult males have two distinct home range areas with multiple core areas within. The territories that the adult males defend in areas of high female densities are constrained by the ability of the male to defend it and are typically quite small. Alternatively, a second adult home range area exists on the southern range front. These are often smaller than the home range areas that exist in the central portion of the range. The smaller home range on the range front could be a result of increased resources within an area that has been less exploited and this would negate the need to travel long distances to find food. There is no pressure on the males, when they are residing in male groups, to do anything but forage and rest. Movement is energetically expensive (Williams 1999), so if resources are plentiful there is no need to move very far.

On the other hand, a majority of adult females, sub-adult males, and sub-adult females have multiple areas of use within one continuous home range. The sub-adult males use a much greater amount of linear coastline than all other classes (Appendix F). Sub-adult males not only use a larger linear area of coastline (~54 km vs. 9 – 15 km for other classes) but also occupy an area extending further from shore than other age/sex classes (~2.5 km vs. 0.8 – 1.1 km for other classes). As a result sub-adult males typically have one continuous home range within which are incorporated multiple areas of use. Thus their calculated home ranges are larger than those of all other classes.

Spatial Variation – Home Range Area

Cambria animals had significantly longer average move lengths over longer time periods (particularly for a year) than animals from the Monterey study and based on these results one would expect home range areas to be larger as well. Indeed, Cambria animals had larger home range areas using all four methods of home range calculation (Table 8).

The same factors that play a role in increased average movement by the Cambria animals are likely influencing the need to use greater areas, *i.e.* relative prey densities. While habitat and densities are similar in both areas to a degree, the prey richness and abundance are lower in the Cambria region compared to Monterey, as noted earlier. The implication is that sea otters need larger areas of habitat to support life in the central and southern portion of the range than they do around the Monterey Peninsula. If it turns out that significant differences occur in prey composition in Cambria, then this might explain why central and southern males make many more long distant moves than those living on and around the Monterey Peninsula.

Temporal Variation – Home Range Area

There were temporal differences in home range areas for sub-adult females. Specifically, home range sizes of sub-adult females varied between 5.3 – 646 km^2 in the 1980s while the home ranges of sub-adult females near Cambria in the present study varied between 0.9 – 14 km^2 depending on method of calculation.

Why did sub-adult females use a much larger home range area in the 1980s? It is likely that there are two reasons for the differences between sub-adult females from current and past populations. First, the earlier study had a relatively equal number of animals for each of the age/sex classes while the current studies are both heavily weighted toward adults. Second, the earlier study captured animals at five different locations along the coast (Figure 14) while all of the sub-adult females from the present study were captured and tracked within 2 km of one another in the Cambria area. This broader spatial representation may mean that the results from the 1980s study are more representative of what sub-adult females do on average.

There is a potential explanation for why the current sub-adults residing in the Cambria area have significantly smaller home ranges. The bathymetry along the Big Sur coast is very different from the bathymetry in Cambria. In many areas along the Big Sur coast, the depth of the water increases dramatically as a result of the coastal shelf ending very close to the shore (Figure 27). South of Cambria the coastal shelf extends out from the shore and as a result there is more shallow water habitat per unit length of shoreline (Figure 28). This may have forced the sub-adult females from the 1980s to utilize a long, narrow, essentially one-dimensional band along the Big Sur coast. Support for this can be seen when the linear shoreline used by the earlier sub-adult females (~18 km) is compared to the Cambria sub-adult females (~4 km). Adult females and sub-adult males in the 1980s also used more linear coastline than their current counterparts (Table 8). Additionally, 1980s animals were also tracked over a greater area than the Cambria animals and this may have contributed to some of the variation in home range size.

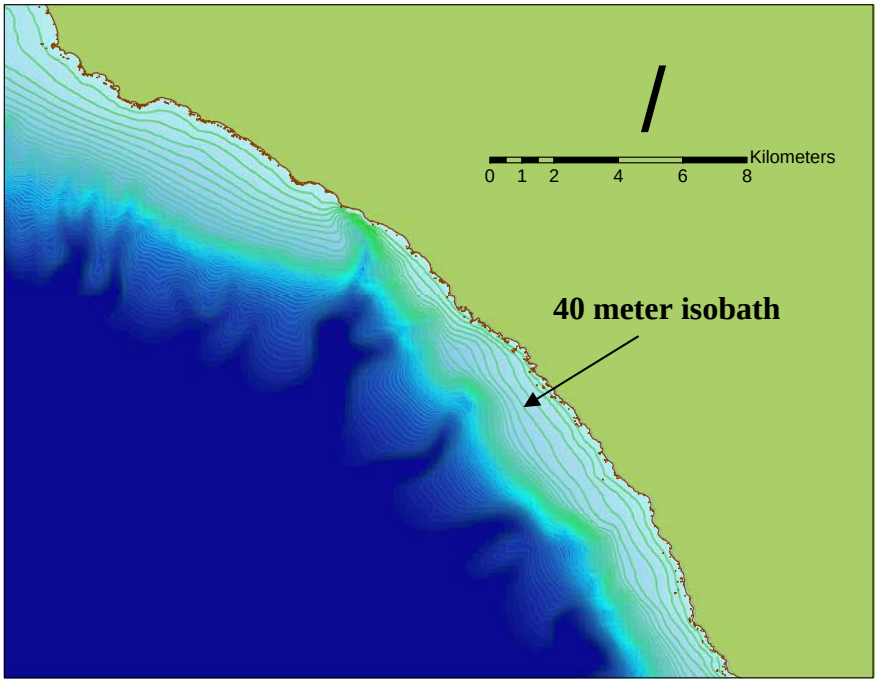

Figure 27. Big Sur coastline where the 40 meter isobath occurs (on average) 750 meters off shore. The 40 meter isobath defines the typical depth range within which sea otters dive to forage**.**

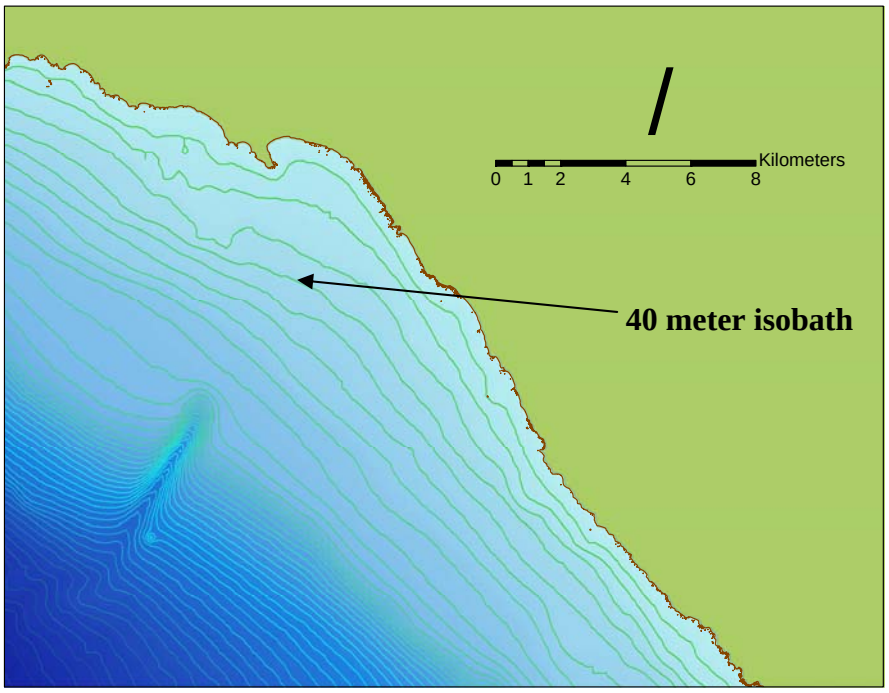

Figure 28. Cambria, CA coastline where the 40 meter isobath occurs (on average) 1.5 kilometers offshore, more than twice the distance of occurrence along the Big Sur, CA coastline.

Variation in Home Range Methodology

As was expected, the MCP method produced larger home range sizes than the other three methods (Table 6). In the past MCP has been the most commonly used method to analyze sea otter home ranges. However, it does not do a good job of estimating home range area and, additionally, it gives no insight into how a sea otter may utilize its habitat (Figure 29). MCP has been shown to be appropriate for calculating home ranges of territorial animals that delineate their ranges with marking behavior (Gubbins 2002) but is much less useful in understanding the biological significance of an animal's home range. MCP is also sensitive to sample size and typically increases as sample size increases (White and Garrott 1990). This sensitivity to sample size would have precluded the use of a majority of the movement locations gathered for each individual and this was one of the reasons for comparing a polygon method to one that used a frequency distribution to calculate home range areas.

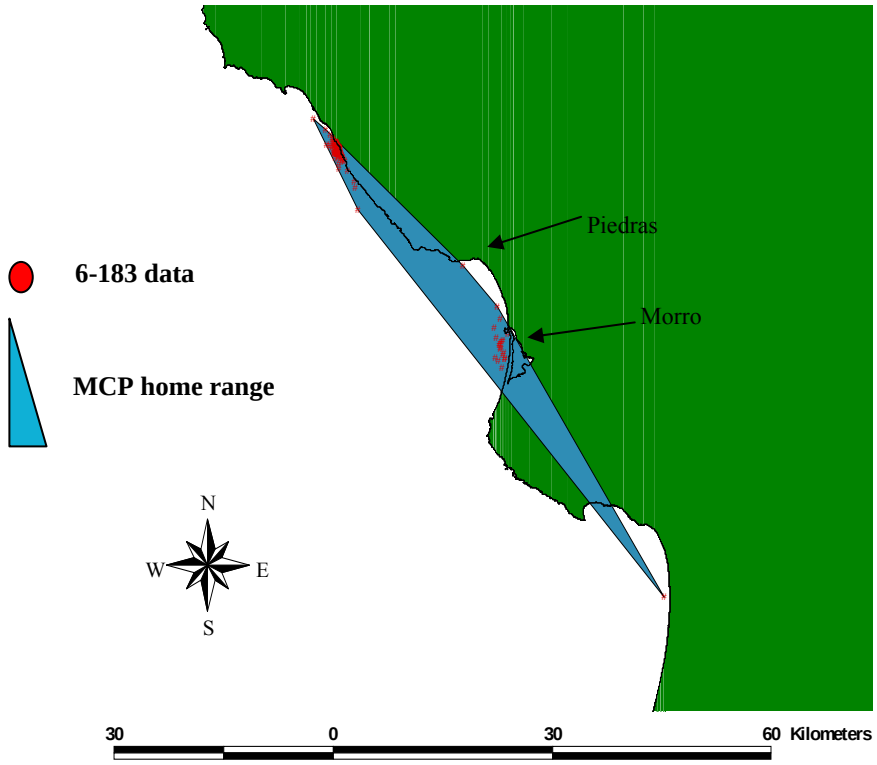

Figure 29. Minimum convex polygon (MCP) home range area (2,834 km^2) for male sea otter 6-183 from the current Cambria sub-population.

AK methods, which calculate home range area based on frequency of occurrence, are not sensitive to large sample size as the size of the area typically levels off and remains unchanged after 50 locations (Millspaugh and Marzluff 2001). As a result, one can use more locations and perhaps gain greater insight into the intensity of use of various parts of an animal's home range with these methods. The frequencies are calculated and form a utilization distribution. The utilization distribution then allows calculation of probability of

occurrence adaptive kernels. These AK home ranges did a better job at estimating areas of core use, or in the case of males, territories.

However, for a nearshore marine species that do not use the terrestrial environment at all, AK has a major drawback. The function in Arc View 3.2 lacks the ability to allow barriers that restrict the use of inappropriate area when calculating the kernel(s). This drawback causes an overestimation of an animal's home range size. The problem can be remedied by subtracting the area of unusable habitat from the overall area of the kernel home range (Figure 30 (a) and (b)). This provides a more precise idea of patterns of use within an animal's home range as well as information on core areas of use. Still, the inability to parameterize the kernel density function in Arc View 3.2 results in kernels that are less likely to accurately reflect correct patterns of use for southern sea otters.

For this reason, CAU home range, an alternative to other home range methods was calculated. Southern sea otters move largely in a linear fashion over one-dimension. Linear shore use has been used as a descriptor of sea otter home range in at least one study in the past (Jameson 1989). Southern sea otters are also usually found within two kilometers of shore. Therefore, in order to gain a better understanding of exactly how much linear shoreline is used by individuals as well as to gain insight into the perpendicular distance off-shore each animal used 95% of the time; a CAU home range was determined and compared to the others (Figure 31). Overall CAU was the smallest calculated area of home range size for all animals (Appendix F). Using AK home range methods to calculate a 95% probability of occurrence kernel and then using the edges of that kernel to interpret the distance an animal uses along the coast is one method that may accurately reflect a linear distance used by the sea otter. AK is not sensitive to outliers and so is less susceptible to biases associated with individuals that make a very few long distance moves, a problem often encountered when using MCP methods. The linear shoreline distance encompassed by the AK polygon may thus provide a less biased index for comparing relative range sizes between and within populations than would be gained by simply measuring the linear shore line encompassed by the raw data cloud or by the MCP.

a) Adaptive Kernel

b) Adjusted Kernel

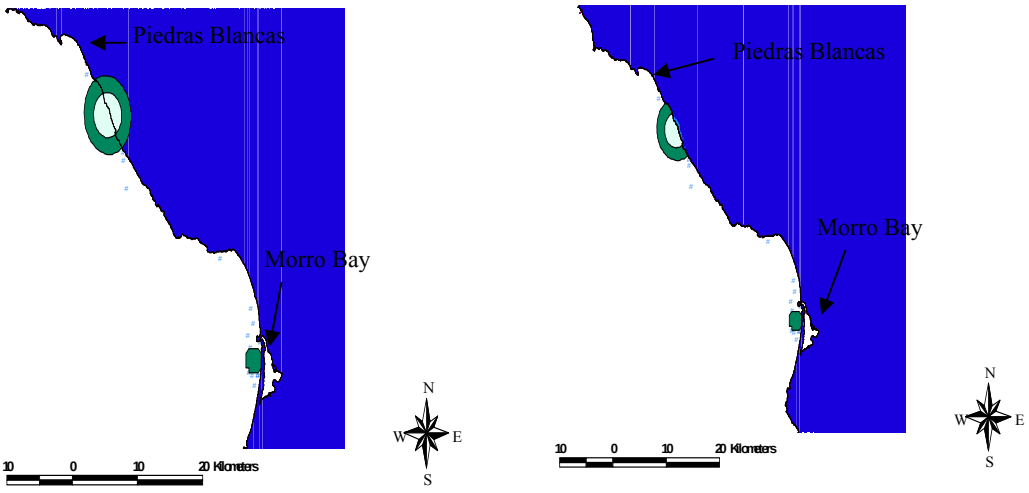

Figure 30. a) 50 and 95% kernels of probability for male sea otter 6-183 from the current Cambria sub-population calculated using adaptive kernel (AK) home range analysis (48.5 km^2), b) 50 95% kernels of probability also for male sea otter 6-183 that has been adjusted to disregard unusable habitat (terrestrial)(29.16 km^2).

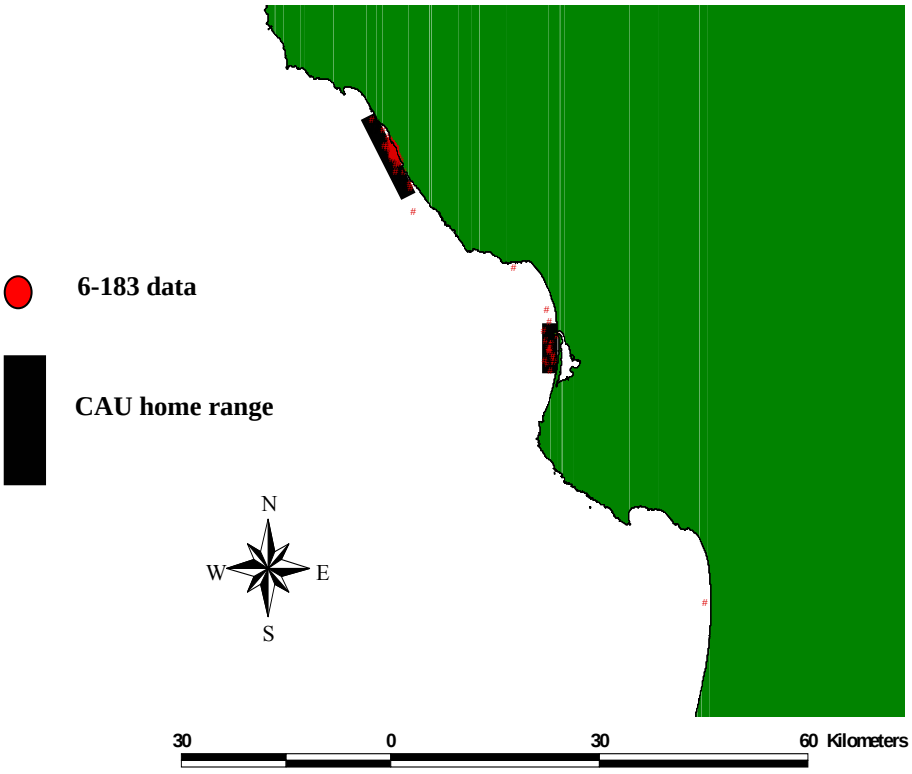

Figure 31. Calculated area of use (CAU) home range polygon (10.5 km^2) calculated from two parameters: linear shore line in which 95 % of locations occurred and offshore area in which 95% of location occurred, for male sea otter 6-183 from the current Cambria sub-population.

If the ability to establish barriers within the AK function in Arc View 3.2, or other GIS software, becomes available, that would make the AK method of home range calculation a better measure of sea otter home ranges. Until that time, for southern sea otters, the best estimation of home range seems to be CAU.

Spatial Variation using Correlated Random Walk

As noted previously, sea otters in the central and southern locations moved longer distances on the average than those in the northern location. However, on a daily time scale animals from these areas had similar move lengths. As a result one would expect a CRW model to make similar predictions for both sub-populations. However, CRW drastically under-predicted the O (Rn^2) for the Cambria study for days one – three but began to do a better job by days four and five (Figure 20). In contrast, the CRW model only slightly under-predicts O (Rn^2) for the Monterey animals over the entire five day subset and this sub-population seems to conform to the model. In other studies, under-prediction of O (Rn^2) indicated non-random turning angles (Turchin 1998, Bergman *et al.* 2000) While this result implies that animals are moving along paths in a more linear fashion than the CRW predicts, it could be

explained if these movements are accomplished by alternating right and left turns in a non-random fashion. In fact, turning angles were decidedly non-random for the Cambria sub-population and much more randomly distributed for the Monterey animals (Figure 32). On the other hand, one of the major assumptions of a CRW model is that animals are able to disperse in a fully two-dimensional world. Southern sea otters move in a much more linear fashion. In other words they are restricted to a somewhat one-dimensional coastline. It is quite likely that by using a full range of turning angles, not just left or right turns, predictions for displacement from the starting point were low and this is possible one of the most important reasons that the model under-predicts observed displacements (Turchin 1998).

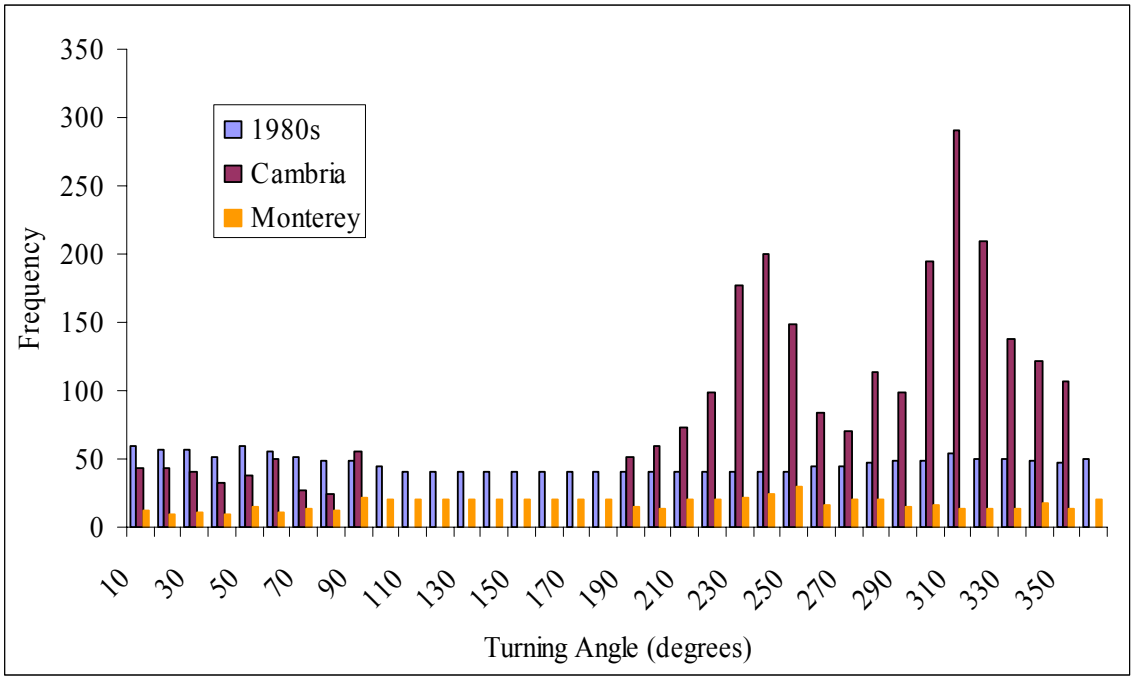

Figure 32. Distribution of turn angles for three studies; 1980s, current Cambria sub-population and current Monterey Bay sub- population of sea otters.

Therefore, under-prediction of displacement by a CRW model is an indication that sea otters are making one-dimensional moves along a linear coastline. However, the model did not under-predict displacement equally for each population. As mentioned, the displacement for the Cambria sub-population was under-predicted vastly more than the other two studies. Perhaps this is an indication that the Cambria animals are making more efficient use of their home range. As movement is energetically expensive (Williams 1999), it is reasonable to expect that it is more efficient for sea otters to take the most direct route possible. In caribou, under-prediction of displacement by a CRW model was indicative of efficient return to calving grounds from wintering sites (Bergman *et al.* 2000). For sea otters, straightened movement paths might be a means of conserving energy. Sea otters live in very cold water and unlike other marine mammals, have little subcutaneous fat to provide warmth. By using direct movement between resting, mating, and foraging areas they may conserve energy by reducing the amount of time required to travel.

Temporal Variation using Correlated Random Walk

There was little difference in daily average move length between the Cambria sub-population and the 1980s population and again, one would expect similar results for the CRW model. The Cambria population was under-predicted by the model (Figure 22). However, data from the 1980s population appear to fit a CRW (Figure 20). Turn angles for the 1980s population were distributed randomly (Figure 32). Even though turn angles were not random for the Cambria study (Figure 32), O (Rn^2) entered the confidence interval for E (RN^2) so non-randomness in turn angle in this case, does not seem to be associated with a lack of suitability of CRW predictions. As a consequence, failure to reject the model does not necessarily imply that the model assumptions are entirely satisfied. It seems that predictions of net squared displacement are much more sensitive to autocorrelations in turning angle than move lengths (Bergman *et al.* 2000). Turchin (1998) also stated that the primary reason for rejecting a CRW as a movement descriptor is because of autocorrelation in turning angles. An assessment of autocorrelations in move lengths and turning angles is the next logical step.

Animals in the 1980s seemed to be turning randomly with much less direction than animals in the current central and southern portion of the range. Animals from all three studies were using similar habitat (rocky substrate with moderate to large amounts of kelp); however, sea otter densities have increased somewhat in the study regions since the mid 1980s. It is possible that increased densities are contributing, at least in part, to more directed movements in the current population. Although the Monterey animals fit the CRW model well, the model did slightly under-predict what they were actually doing. Densities are similar in both of the current study areas (Cambria and Monterey) and both exhibit similar movement patterns on a daily basis, yet the model was a much better fit for the Monterey animals. The less directed movement of the 1980s population may also be indicative of a habitat that had relatively more abundant food that was more uniformly distributed in space and time than current habitat.

Zollner (1999) used theoretical simulation modeling to predict that movement described by a CRW model should increase the likelihood of successful dispersal. The results from the 1980s CRW model qualitatively support this theory. Knowledge of sea otter range use indicates that from 1987 to around 2001 the southern range edge continued to increase. Alternative support for this theory comes by examining the Cambria and Monterey CRW model results. The Monterey population was slightly under-predicted by the CRW model and the Cambria population was drastically under-predicted in the beginning of the time series so neither study conformed as ideally as the 1980s animals.

Range expansion of the sea otter, to both the south and the north, has stagnated or even slightly receded since 2001 (B. Hatfield USGS pers. comm. 2004). That current otters do not conform to the CRW model as well as they did in the 1980s may be an indicator that animals are not dispersing as successfully as in the past and as a result range expansion has slowed or ceased. However, multiple factors likely are affecting the current trend in range expansion. Factors such as spatial characteristics of habitat (*i.e.* substrate type and bathymetry), along with intrinsic factors such as culture, likely influence the movement

patterns of sea otters. These factors are not accounted for by theory and therefore cannot be explained by CRW.

Conclusions

The success of describing the movement of two subsets of a marine carnivore population using empirical data along with CRW theory could assist in more innovative modeling of population dispersal through the environment (Turchin 1998). It seems logical to think that the use of empirical individual movement data could lead to more applicable rules that dictate what choices are made in theoretical simulation modeling. The accomplishment of using generalized movement parameters (move length and turn angle) and not those specified for a particular species, as often happens in modeling, allows for a potential use by managers for a variety of mammalian carnivores and other vertebrates. By linking marine carnivore movements to other models, (*i.e.* resource use, dispersal, foraging, and searching strategy), ecologists could potentially portray the dynamics of a marine reserve-keystone predator at large spatial scales. With each success or failure, the likelihood that such models could and would be tested across a variety of species and habitats increases. For periods in which the model fails, an examination into autocorrelations and independence of the data may suggest what alternative models to use (Bergman *et al.* 2000).

An important methodological question in any ecological study concerns appropriate sample sizes: how much is enough to accurately describe the species? Southern sea otter age/sex classes move very differently over different time periods for a variety of reasons. By determining that sea otter movement should be studied for at least three months in order to gain representative estimates of movement rates and home range size, this study provides a valuable tool for managers and conservationists in future sea otter studies. These results may also help researchers studying movements in other mammalian carnivores, providing guidelines on useful techniques and sample sizes necessary to adequately characterize movement patterns in a mammalian carnivore.

Future work is needed in a variety of areas to build upon the results of this study. For instance, invertebrate sampling for prey composition and species richness between study areas would allow a better understanding of differences in move lengths and home range area between the studies. It could also determine the relative patchiness of each area and provide insight into the role that fragmentation has on how a population moves in its environment.

In particular, for southern sea otters, CRW should be applied to longer time periods. If the CRW model gives a good description of movement over 15 days, a month, or even a year, it will increase the value of these movement parameters as descriptors and allow the use of this model to give an indication of what range expansion might be expected in the future. CRW theory should also be tested on foraging movement and searching behavior of sea otters to give empirical support to the theoretical simulation models that suggest CRW models would be an accurate descriptor for these behaviors (Turchin 1998, Zollner and Lima 1999). It is also important to test whether a CRW model is a valid means of analyzing movement of other mammalian carnivores. The limited success of this model with southern sea otters

perhaps can provide the first step to encourage other researchers, studying similar species, to try and determine if CRW and other individual based movement models can be used to accurately describe movement patterns in their species of interest. With every success or failure in which empirical data is applied to theory, scientists are one step closer to understanding another piece of the puzzle in the ecology of a species and its influence on its surrounding community.

Chapter 4. A Spatially Explicit Simulation Model to Predict Southern Range Expansion

M. Tim Tinker, Daniel F. Doak, James A. Estes, Alisha H. Kage

Abstract

1. Reliable projections of future population growth and southward range expansion of the southern sea otter population would be useful for a number of management purposes, and are of interest to several state and federal agencies, including MMS.
2. We developed a spatially explicit simulation model to project population growth and southward range expansion. Our model represents a unique synthesis of a multi-state dispersal matrix with the integrodifference equation approach to calculating invasion speed. The model was parameterized with data from the current study.
3. We used the results of repeated simulations with this model to predict future patterns of range expansion while accounting for uncertainty in model parameters. Although model output closely matched historical data on rates of southward range expansion, simulation results were highly variable, reflecting the uncertainty of estimates of input parameters as well as the uncertainty regarding ultimate causes of variation in survival rates.
4. Males are more likely than females to move long distances, and most of the individuals that travel south of Point Conception are males, yet movement rates of females, particularly those of juvenile and sub-adult females, had much more impact on both population expansion and southward range expansion than those of males.
5. The survival rate of juvenile/sub-adult females in the southern part of the range emerged as a key parameter influencing the rate of range expansion. Fieldwork to improve estimates of this parameter would do much to reduce uncertainty in the model's predictions.
6. Although our model is relatively simple and does not account for many important aspects of sea otter biology and ecology, it makes use of all existing demographic and movement data and provides a robust and generalizable approach to understanding and predicting population dynamics in southern sea otters. This new tool for conservation biologist and managers can be easily expanded and improved as additional data and more precise parameter estimates become available.

Introduction

Data on age- and sex-specific probabilities of survival, reproduction and movement provide the basic tools for understanding past and present population dynamics (Caswell 2001, Doak and Morris 2002), and can also be used for predicting future population dynamics. Such tools are often the basis for conservation and management decisions. In the case of the southern sea otter, developing a realistic projection of future population growth and range expansion at the southern end of the current distribution would facilitate the informed assessment of potential impacts of sea otters on important industries (e.g. fisheries, eco-tourism), potential negative effects of human activity on sea otters (e.g. risks associated with the near-shore transport and extraction of petroleum, entanglement in fishing gear, etc.), and the eventual recovery and de-listing of this threatened species (USFWS 2003). One of the most important outcomes of the current research efforts has been the accumulation of a detailed and extensive database of spatially-explicit demographic and movement information for the southern sea otter. Here, we use these data to develop a spatially structured simulation model for predicting population growth and southward range expansion.

Stage-based projection matrices provide a means of integrating information on population structure, individual survival and reproduction in an intuitive and mathematically useful way. Projection matrices are commonly used to predict future population dynamics, measure the sensitivity of these dynamics to particular vital rates, and elucidate the underlying processes responsible for patterns of interest (Caswell 2001). Multi-state projection matrices represent an extension of the basic matrix approach, and can be utilized when population structure or environmental conditions vary with geographic location, or when the effects of individual movements between sub-populations are thought to be important (Lebreton and Gonzalez-Davila 1993). Multi-state projection models facilitate the quantitative interpretation of source-sink dynamics (e.g. Doak 1995), and can help to clarify the relative importance of survival and dispersal in driving population trends (e.g. Lebreton and Gonzalez-Davila 1993).

Multi-state matrices are often used to study metapopulation dynamics and the colonization rate of unoccupied habitat (Caswell 2001). The latter phenomenon can also be modeled as a continuous variable using integrodifference equations, as described by Neubert and Caswell (2000). This relatively new technique utilizes stage-specific data on dispersal and vital rates to derive the asymptotic speed at which the population front (or "traveling wave") will invade empty habitat (Neubert and Caswell 2000). Note that for the purpose of our analyses we will define the term "dispersal" in a purely quantitative, descriptive sense, referring to the average linear distance moved (or mean net displacement) between the location of an individual at time t=1 and the location at t=2. This definition makes no reference to the biological cause or behavioral significance of the movements, which may often differ between age and sex classes.

In the case of the southern sea otter, analyses of multiple data sets indicate that demographic rates are not constant across the sea otters range, but vary between broad geographic areas (Figure 33; Chapter 2, this report). Moreover, it appears that individual dispersal distances also vary by age and sex class (Chapter 3, this report). A multi-state projection matrix model would therefore be an appropriate tool for elucidating the relative importance of dispersal

and survival in driving population dynamics at the range peripheries. The interaction between stage-specific dispersal and vital rates will also likely determine the rate and pattern of population expansion into unoccupied territory, a phenomenon best described using integrodifference equation models (Neubert and Caswell 2000). We couple these two techniques in a spatially explicit simulation model, parameterized using data from the current study (Chapter 2, this report), and use the results of repeated simulations to predict future patterns of range expansion while accounting for uncertainty in model parameters. We then use sensitivity analysis to determine the relative importance of each model parameter, in order to highlight specific areas where further study will be particularly useful.

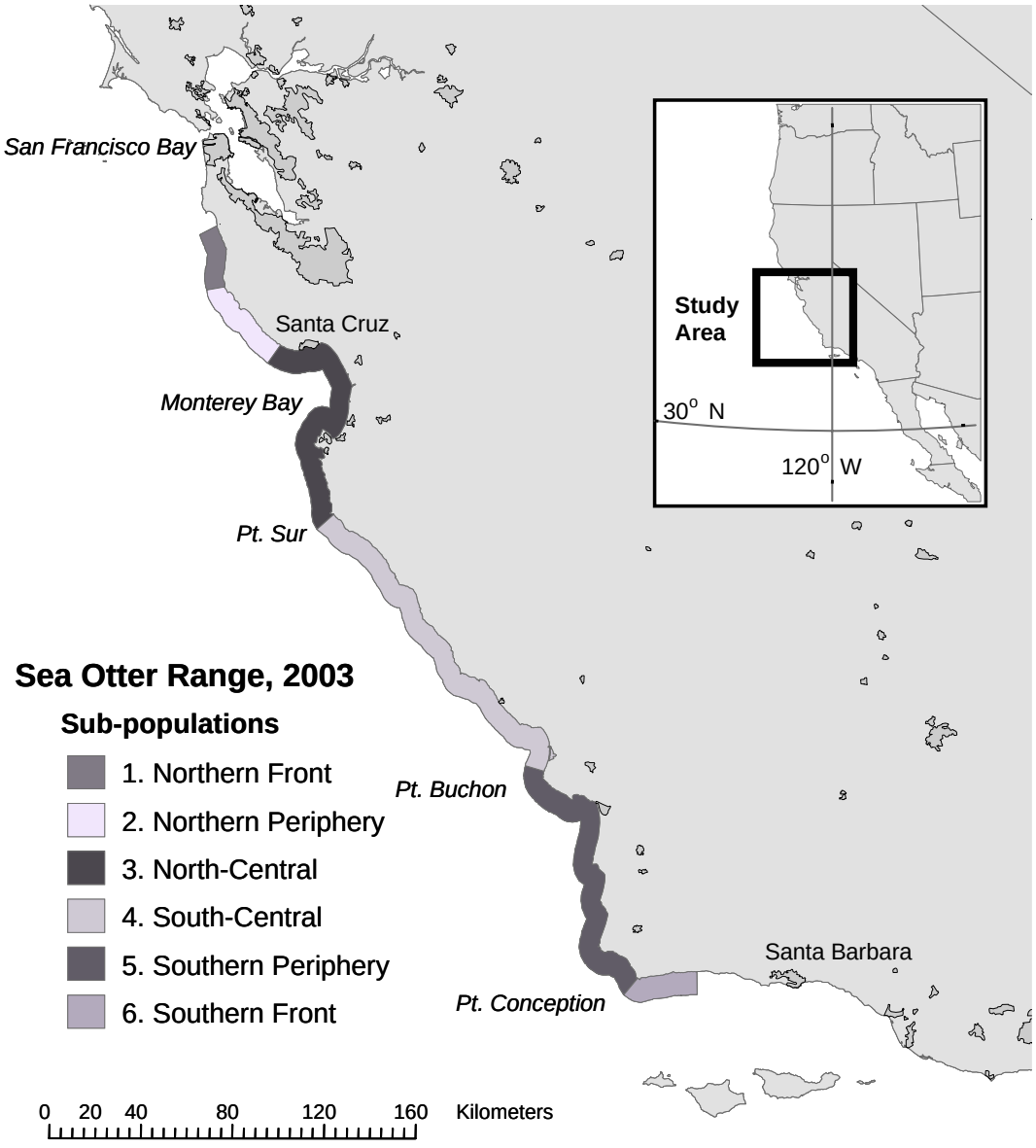

Figure 33. Map of central California showing current range of the southern sea otter (excluding San Nicolas Island), and identifying the spatial arrangement of the six sub-populations identified for the simulation model.

Methods

Matrix Structure

A stage-based, 2-sex projection matrix (Caswell 2001) was used to describe annual transitions between 4 age-classes: juveniles (defined as 1 year post-weaning), sub-adults (2 and 3-year-olds), prime-age adults (4–10-year-olds) and aged adults (11 years of age or older). Specifically, we constructed an 8×8 matrix of the form:

$$\mathbf{A} = \begin{array}{c|cccc|cccc} & \multicolumn{4}{c|}{\text{Sex = f}} & \multicolumn{4}{c}{\text{Sex = m}} \\ \text{Sex = f} & 0 & R_{1,2} & R_{1,3} & R_{1,4} & 0 & 0 & 0 & 0 \\ & G_{2,1} & P_{2,2} & 0 & 0 & 0 & 0 & 0 & 0 \\ & 0 & G_{3,2} & P_{3,3} & 0 & 0 & 0 & 0 & 0 \\ & 0 & 0 & G_{4,3} & P_{4,4} & 0 & 0 & 0 & 0 \\ \hline \text{Sex = m} & 0 & R_{5,2} & R_{5,3} & R_{5,4} & 0 & 0 & 0 & 0 \\ & 0 & 0 & 0 & 0 & G_{6,5} & P_{6,6} & 0 & 0 \\ & 0 & 0 & 0 & 0 & 0 & G_{7,6} & P_{7,7} & 0 \\ & 0 & 0 & 0 & 0 & 0 & 0 & G_{8,7} & P_{8,8} \end{array} \qquad 30$$

where each element of **A**, $a_{j,i}$, represents the transition from age/sex class i to age/sex class j. Note that $i \leq 4$ correspond to female age-classes, while $i \geq 5$ correspond to male age classes. Three types of transition are identified in **A**: *G, P* and *R*. The first type of transition, *G*, represents survival and growth: in other words, the probability that individuals survive for 1 year and advance to the next age-class. The second type, *P*, represents "persistence", or survival without transition to the next age class. The final type of transition, *R*, represents survival and successful reproduction: for our purposes, an individual female is considered to have successfully reproduced if she gives birth and successfully weans a pup (i.e. she contributes a single viable juvenile to the population).

To estimate *P*, *G* and *R* we used standard equations for deriving fixed-stage-duration transition probabilities from underlying vital rates (Caswell 2001):

$$P_{i,i} = s_i \cdot \left(1 - \frac{(s_i/\lambda)^{T_i} - (s_i/\lambda)^{T_i - 1}}{(s_i/\lambda)^{T_i} - 1}\right) \qquad 31$$

$$G_{j,i} = s_i \cdot \left(\frac{(s_i/\lambda)^{T_i} - (s_i/\lambda)^{T_i - 1}}{(s_i/\lambda)^{T_i} - 1}\right) \qquad 32$$

$$R_{j,i} = s_i \cdot \tfrac{1}{2} b_i \cdot w_i \qquad 33$$

where T_i is the stage duration (in years) for age/sex class i, λ is the annual rate of population growth, s_i is the annual survival rate for an individual of stage i, b_i represents the birth rate

for a female of stage i and w_i represents the weaning success rate for a female of stage i. We assumed a 1:1 sex ratio at birth.

Matrix **A** was used to model the basic demographic processes for sea otters at a particular time and place. The next step was to introduce spatial structure to the model by constructing a multi-state matrix. Consider a structured population consisting of three sub-populations, each of which exhibits unique demographic properties, and between which there is no potential for dispersal. A multi-state matrix for such a population would be:

$$\mathbf{B} = \begin{matrix} A_{1,1} & 0 & 0 \\ 0 & A_{2,2} & 0 \\ 0 & 0 & A_{3,3} \end{matrix} \qquad 34$$

where each cell of matrix **B** represents a transition from sub-population x to sub-population y. The diagonal of **B** consists of sub-matrices $\mathbf{A_{y,x}}$ (where $y = x$), each of which describes demographic processes for a single sub-population according to equation 30. All other elements of **B** are set to 0 because we specified no dispersal between sub-populations.

Unfortunately, although equation 34 is conceptually very simple, it is also unrealistic: for more realistic dynamics we must allow dispersal between sub-populations. Accordingly, let $m_{i,x\to y}$ represent the probability of moving to sub-population y for an individual of stage i that starts the year in sub-population x. These probabilities can be incorporated into a new matrix, **M**, that has a general structure identical to **A** but whose elements correspond to stage-specific dispersal probabilities ($m_{i,x\to y}$) rather than survival or reproduction. Dispersal probabilities between sub-populations can be calculated from empirically-derived dispersal distance distributions. We assumed that the annual dispersal distance for an individual sea otter of stage i at location x' (i.e. somewhere within sup-population x) could be described by a Laplace probability distribution with shape parameter $\sigma_{i,x}$. The Laplace distribution essentially consists of two back-to-back exponential distributions, and was considered appropriate for modeling sea otter movements in California because animals are restricted to dispersal in one of two directions (north or south along the coast).

We defined each sub-population spatially by its northern and southern boundaries along the ATOS line (the "as the otter swims" line, corresponding to a series of points at 500m increments, north to south, along the 10m bathymetric contour); thus sub-population y was spatially defined by boundary points y_N and y_S, and spanned $0.5(y_S - y_N)$ km of coastline. The probability that an individual located at point x' would disperse to sub-population y was estimated as the absolute difference between the Laplace cumulative distribution function evaluated at values $y_N - x'$ and $y_S - x'$:

$$m_{i(x')\to y} = \left| \left(1 - \frac{1}{2}\exp\left(\frac{y_N - x'}{\sigma_{i,x}}\right)\right) - \left(1 - \frac{1}{2}\exp\left(\frac{y_S - x'}{\sigma_{i,x}}\right)\right) \right| \qquad 35$$

and the net probability of dispersal from sub-population x to sub-population y was estimated as:

$$m_{i,x\to y} = \sum_{x'=x_N}^{x_S} \left(m_{i(x')\to y}\right) p(x') \qquad 36$$

where $p(x')$ sums to 1 for $x_N \le x' \le x_S$ and represents the probability that an individual animal from sub-population x would be located at x'. For simplicity we used discreet summation, rather than continuous integration, thereby assuming that all points within a 500m interval (or ATOS unit) would be adequately represented by a single integer value of x'. A uniform spatial distribution of individuals within each sub-population would have allowed us to define $p(x') = 1/(x_S - x_N + 1)$; however, examination of annual range-wide survey counts suggested that sea otters were not uniformly distributed but were often skewed towards one boundary or clumped within one region. To account for this non-uniformity, we used beta probability functions to represent the spatial distribution of otters within each sub-population. Specifically, we fit beta distributions to the raw survey data for each sub-population (using data from the 5 most recent spring counts; Figure 34), having first standardized the location data to values between 0 and 1 (where 0 corresponded to the northern boundary and 1 corresponded to the southern boundary of the sub-population). Using the resulting beta functions we could then calculate the probability that an individual from sub-population x would be located at x':

$$p(x') = \beta\left(a, b, \frac{x' - x_N + 1}{x_N - x_S + 1}\right) - \beta\left(a, b, \frac{x' - x_N}{x_N - x_S + 1}\right) \qquad 37$$

where $\beta(a,b,Z)$ represents the beta cumulative distribution function with parameters a and b, evaluated at value = Z.

Equations 35 – 37 were solved for each pair of sub-populations, including the special case when $y = x$ (which corresponds to the probability of remaining within the same sub-population). To ensure that $\sum m_{i,x\to y} = 1$ for each combination of i and x, we made the simplifying assumption that individuals whose dispersal distance brought them to the range end would "bounce off" this boundary. This was accomplished by a minor adjustment to equation 35 when the target sub-population was a range end: when the target was the northern-most end of the range, $y_N - x'$ was set to ∞, and when the target was the southern-most end of the range, $y_S - x'$ was set to ∞.

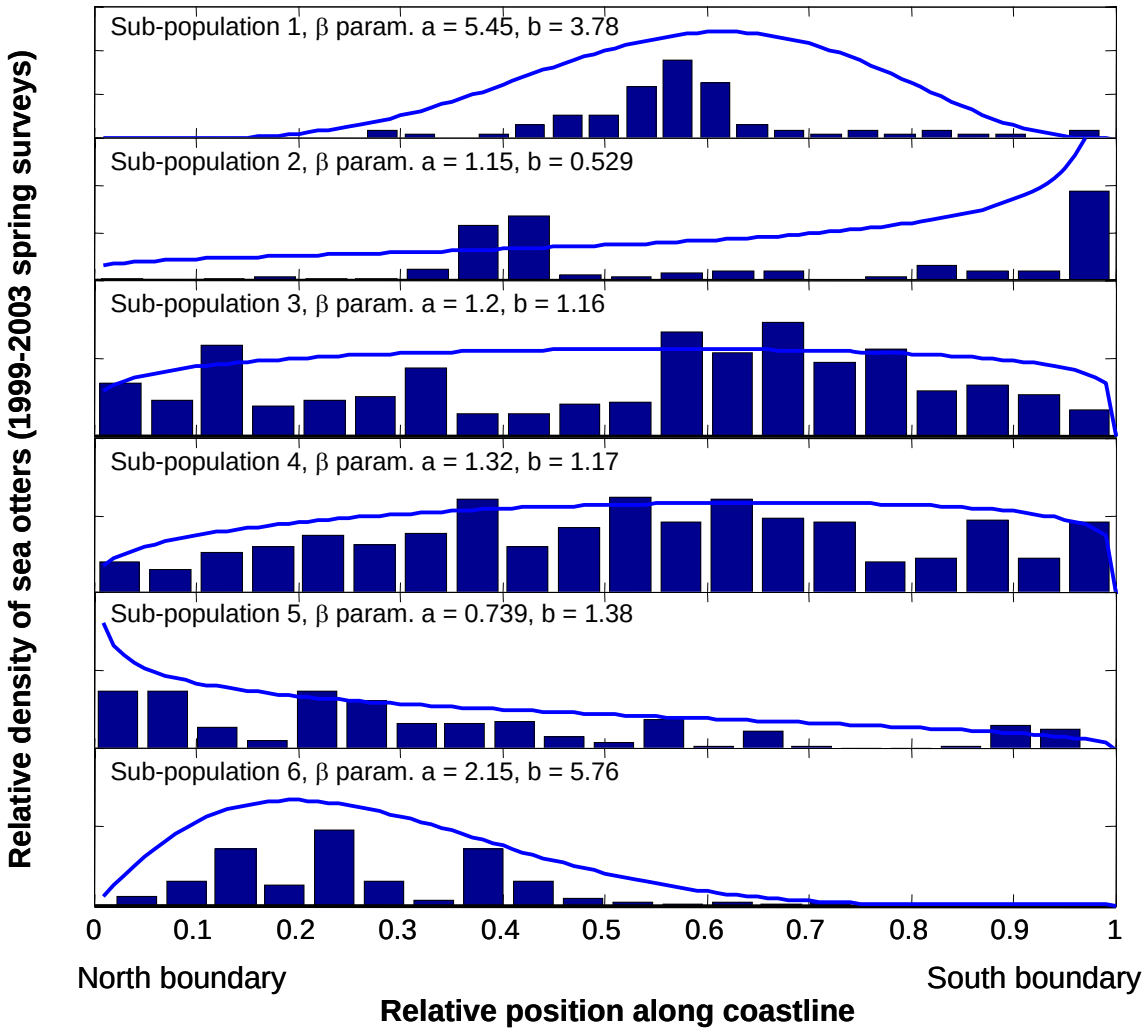

Figure 34. The spatial distribution of sea otters along the coast (on a north-to-south axis) is plotted as a histogram for each of the six sub-populations (see Figure 1), based on the results of the five most recent spring surveys. *Beta* probability density functions were fit to each data set and are overlain on the histograms: the parameter values for each function are displayed above each curve. The *Beta* functions were used in the calculation of movement rates between sub-populations (see text).

Combining the two types of matrix, **M** and **A**, we constructed a multi-state matrix which allowed for movements between sub-populations (illustrated again with just three sub-populations for simplicity):

$$\mathbf{B} = \begin{matrix} A_{1,1} \circ M_{1,1} & A_{1,2} \circ M_{1,2} & A_{1,3} \circ M_{1,3} \\ A_{2,1} \circ M_{2,1} & A_{2,2} \circ M_{2,2} & A_{2,3} \circ M_{2,3} \\ A_{3,1} \circ M_{3,1} & A_{2,3} \circ M_{2,3} & A_{3,3} \circ M_{3,3} \end{matrix} \qquad 38$$

Each cell of matrix **B** consists of the Hadamard product of a demographic matrix and a movement matrix ($\mathbf{A_{y,x}} \circ \mathbf{M_{y,x}}$, where $\circ$ represents element-by-element multiplication). The

resulting elements of each sub-matrix therefore represent joint probabilities of moving from *x* to *y* and then successfully making the transition from stage *i* to stage *j*. Note that the diagonal of **B** is mathematically identical to all other cells, though it actually represents the special case where individuals do not disperse. For computational simplicity we required that individuals disperse at the start of each new year, after which survival, growth and reproduction occur at the new location: this results in a demographic sub-matrix $\mathbf{A_{y,x}}$ that is identical for all cells in a given row of **B**.

Simulating Range Expansion

The multi-state matrix model in equation 38 accounts for dispersal and demographic processes within the existing range of the southern sea otter at time *t*. It does not, however, account for the expansion of the existing range boundaries to the north and south. In order to predict the expansion of the population into un-occupied territory, we developed an integrodifference equation model (Neubert and Caswell 2000). This approach utilizes a stage-based demographic matrix, in conjunction with the moment generating functions of stage-specific dispersal kernels (in this case, the Laplace distribution functions described above) to solve for the asymptotic speed of the "traveling wave" formed by the population front as it moves into empty habitat. The asymptotic wave speed has been found to correspond well to the rate of population range expansion in both numerical simulations and empirical data sets (Neubert and Caswell 2000); we therefore used it to estimate the rate at which the range boundaries of the sea otter population will move to the south and north over time.

To predict southward range expansion, we populated demographic matrix **A** with vital rates corresponding to the southern-most sub-population, and used this in conjunction with the appropriate Laplace distribution parameters to solve the integrodifference equation for the asymptotic wave speed, following the methods outlined by Neubert and Caswell (2000). We used the same approach to predict northward range expansion, using vital rates and dispersal kernels corresponding to the northern-most sub-population. The resulting estimates of range expansion speed were used to re-set the northern-most and southern-most sub-population boundaries on an annual basis; this of course had the effect of altering the predicted rates of dispersal to and from these sub-populations, and so equations 35 through 38 were re-solved after each year of population projection.

Model Parameterization

The results of maximum likelihood analyses of mark-recapture data and 10 years of carcass age structure data (see Chapter 2) suggest that the southern sea otter population consists of 4 sub-populations, identified based on consistent differences in vital rates: these correspond to the northern, north-central, south-central and southern portions of the current sea otter range (Figure 33). We identify 2 additional areas for the purpose of this simulation: these are the population "frontal" areas, defined as recently-occupied areas at the northern and southern ends of the range that are currently utilized seasonally and exclusively by males (each frontal area spans 30 km of coastline; Figure 33). The resulting 6 sub-populations were defined spatially as follows:

1. Northern front, North of Pigeon Pt. (ATOS 90–149)
2. Northern periphery, Pigeon Pt. – Santa Cruz (ATOS 150–230)
3. North-central, Santa Cruz – Pt. Sur (ATOS 231–500)
4. South-central, Pt. Sur – Pt. Buchon (ATOS 501–844)
5. Southern periphery, Pt. Buchon – Pt. Conception (ATOS 845–1110)
6. Southern front, South of Pt. Conception (ATOS 1111–1170)

Note that the ATOS outer boundaries for 1 and 6 correspond to the current range limits (2003–2004), and were used to initiate forward simulations. We define the southern and northern range boundaries as the two points on the ATOS line spanning 99.5% of the spring survey count (allowing for up to 4 outlying individual animals at each end), recognizing that this is somewhat arbitrary and that some animals will occasionally be observed well beyond these boundaries. Also, we assumed that sea otters in the frontal areas would exhibit identical vital rates to those in the neighboring sub-populations (although the age/sex structure would be different). Thus vital rates from sub-population 2 were used to parameterize 1, and vital rates from 5 were used to parameterize 6.

To account for uncertainty associated with future population dynamics we used a re-sampling approach, utilizing the range of available vital rate estimates to parameterize the demographic matrices uniquely for each new simulation. Analyses of carcass age structure data provided 10 years (1992-2001) of estimates for each sub-population (Chapter 2). Mark-recapture analyses of telemetry provided two more sets of estimates, one for the 1980's (Siniff and Ralls 1988, Siniff and Ralls 1991) and one for 2001–2003 (Chapter 2). Accumulating evidence suggests that there has been very little variation in reproduction parameters over the past 20 years, so we used a single set of age-specific rates for all simulations: these were set according to the birth rates and weaning success rates calculated from radio-tagged study animals at San Simeon (Chapter 2) and were also consistent with values reported in the literature (Siniff and Ralls 1991, Jameson and Johnson 1993, Riedman et al. 1994). All of the estimates for demographic parameters that we used for simulations are summarized in Table 10.

Table 10. Parameter estimates used for the simulation model. Numbers in parentheses (following mean values) are standard errors, while two numbers seperated by a hyphen indicate the range of values used in simulation runs.

Model Parameter	Juveniles	Sub-adults	Adults	Aged Adults
Annual birth rates	0	0.4	0.98	0.9
Wean success rates	0	0.4 (0.10)	0.061 (0.07)	0.8 (0.07)
Female annual survival rates				
Estimates 1-10: see Ch. 2, Appendix B				
sub-populations 1-2	0.838 - 0.858	0.847 - 0.869	0.843 - 0.870	0.509 - 0.556
sub-population 3	0.833 - 0.853	0.842 - 0.864	0.836 - 0.866	0.504 - 0.550
sub-population 4	0.847 - 0.867	0.854 - 0.876	0.847 - 0.874	0.505 - 0.554
sub-populations 5-6	0.848 - 0.869	0.856 - 0.878	0.849 - 0.876	0.508 - 0.557
Estimate 11: 2001-2003 [1]				
sub-populations 1-2, 5-6	0.85 (0.145)	0.88 (0.145)	0.91 (0.088)	0.55 (n/a)
sub-populations 3-4	0.84 (0.060)	0.84 (0.060)	0.84 (0.060)	0.55 (n/a)
Estimate 12: 1980's, all sub populations	0.85 (0.145)	0.88 (0.145)	0.91 (0.088)	0.55 (n/a)
Male annual survival rates				
Estimates 1-10: see Ch. 2, Appendix B				
sub-populations 1-2	0.782 - 0.809	0.782 - 0.811	0.746 - 0.784	0.328 - 0.371
sub-population 3	0.776 - 0.802	0.776 - 0.805	0.739 - 0.778	0.322 - 0.365
sub-population 4	0.793 - 0.820	0.791 - 0.821	0.751 - 0.791	0.324 - 0.370
sub-populations 5-6	0.795 - 0.822	0.794 - 0.823	0.754 - 0.793	0.327 - 0.373
Estimate 11: 2001-2003 [1]				
sub-populations 1-2, 5-6	0.88 (0.179)	0.88 (0.179)	0.87 (0.095)	0.35 (n/a)
sub-populations 3-4	0.88 (0.179)	0.88 (0.179)	0.84 (0.060)	0.35 (n/a)
Estimate 12: 1980's, all sub populations	0.88 (0.179)	0.88 (0.179)	0.70 (0.167)	0.35 (n/a)
Laplace Dispersal Parameters (σ) [2]				
Females, all sub-populations	32.6 - 83.1	32.6 - 83.1	7.5 - 11.7	7.5 - 11.7
Males, sub-population 1–3	63.2 - 171.0	63.2 - 171.0	7.6 - 20.6	7.6 - 20.6
Males, sub-population 4	63.2 - 171.0	63.2 - 171.0	39.5 - 95.9	39.5 - 95.9
Males, sub-populations 5–6	63.2 - 171.0	63.2 - 171.0	79.7 - 150.0	79.7 - 150.0

[1] Estimates correspond to 1980-'s values for locations or stages not measured in 2001-2003

[2] Units = 500m increments (ATOS values)

Movement probabilities were parameterized by fitting Laplace probability distributions to annual dispersal distances that had been recorded from radio-tagged study animals (Figure 35).

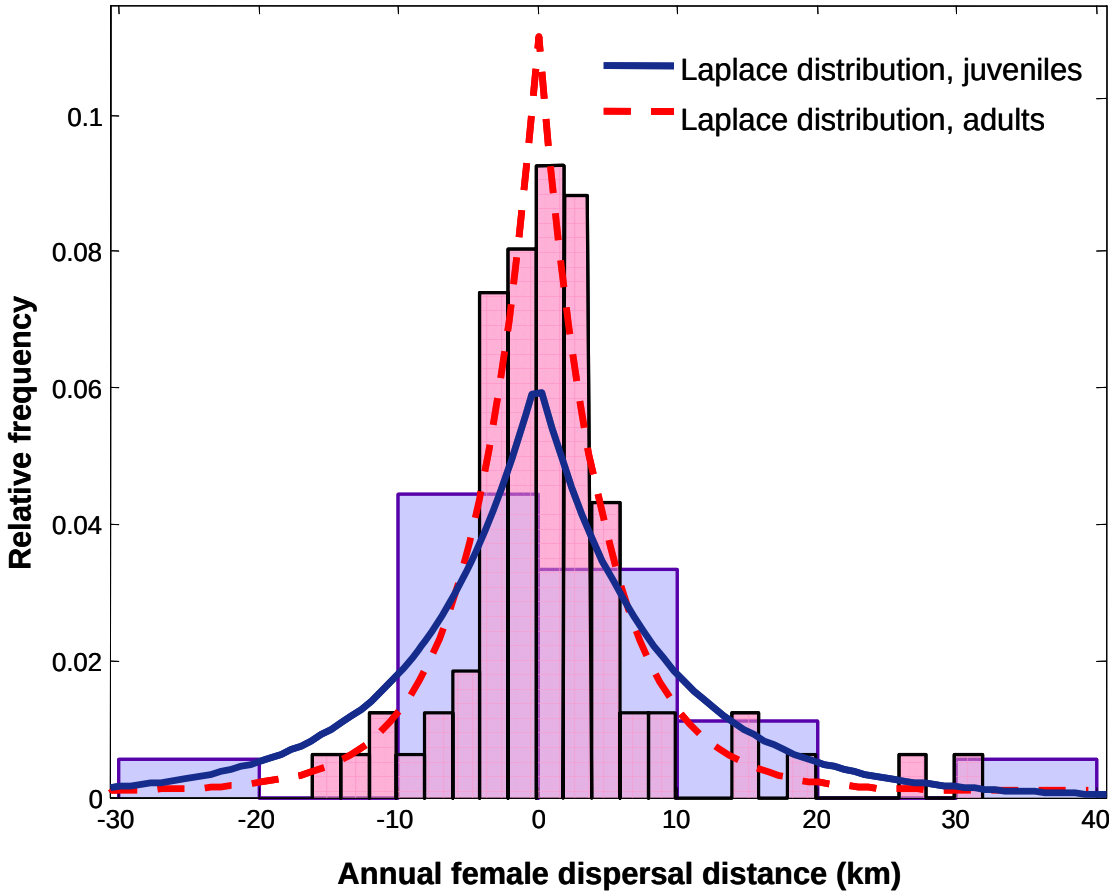

Figure 35. Annual dispersal distance frequency histograms are shown for adult females (pink bars) and juvenile females (blue bars). Laplace probability functions were fit to each of these distributions (dashed and solid lines), and used in the calculation of stage-specific movement rates. Note that the distribution for juvenile females shows greater dispersion, which is reflected by a higher value of the scale parameter σ. Similar functions were calculated for males (not shown here).

Raw data were available for 72 study animals from the current study, with movements restricted primarily to the south half of the range; these data were augmented by data from a concurrent study in the north half of the range (Bodkin and Staedler, unpublished data) and from a similar telemetry study in the 1980's (Siniff and Ralls 1988, Ralls et al. 1996). Further details about the collection and analyses of movement data can be found in Chapter 3. For this particular analysis we used maximum likelihood methods to fit probability distributions for 4 age/sex classes: juvenile/sub-adult females, adult females, juvenile/sub-adult males and adult males. The juvenile/sub-adult age classes and adult/aged-adult age classes were pooled because there were insufficient sample sizes (particularly for juveniles) to allow calculation of separate distributions. Dispersal distance kernels were calculated separately for the north half and south half of the range, and for the southern range front in the case of males. Preliminary analysis indicated that only the data for adult males differed significantly between sub-populations, and so data were pooled across areas for the other age/sex classes. For each probability distribution we calculated the 95% confidence

intervals around $\sigma_{i,x}$ (Table 10), and used this range of values to parameterize movement matrices and dispersal kernel functions.

Running Simulations

Projecting population dynamics can be accomplished simply by matrix multiplication with a population vector. The population vector consists of the number of animals in each stage-class, thus the vector length must equal the number of rows in the projection matrix: in this case, 8 values (4 stages for each sex) for each sub-population, giving a total length of 48. One common way to initialize such a population vector is to multiply an estimate of population size (in this case the survey count for 2003) by the stable stage distribution (SSD) calculated from the matrix using standard algebraic techniques (Caswell 2001). However, this approach requires the assumption that demographic rates have been approximately stable for long enough that the age distribution has converged on the SSD: in the case of the southern sea otter, there is considerable evidence that this has not been the case (Estes et al. 2003a). Consequently, prior to running forward simulations (i.e. to project future population growth and range expansion), it was necessary to run a historical or "hind-cast" simulation to initialize the age-structure for each sub-population. To accomplish this, we utilized the historical demographic rates presented in Table 10 to simulate population dynamics from 1989 to 2003.

We initialized the 1989 population vectors for each sub-population by multiplying the 1989 spring census count by the SSD associated with the 1980's demographic rates (Table 10, estimate 12). Movement matrices were parameterized using the best-fit dispersal kernels for each age/sex class. We then projected 14 years of population dynamics (Figure 36), calculating all demographic transitions, dispersal and range expansion rates as explained above. We adjusted the demographic rates for the 4^{th}–14^{th} years of the projection (1992 to 2003), setting them to equal the appropriate maximum likelihood estimates (Chapter 2; Table 10, estimates 1–11). The outcome of this historical projection was an expected population vector for 2003, which was used to initialize stage distributions for all forward simulations. An additional result was a comparison of expected vs. observed population counts and expected vs. observed range expansion, which we used as a way of graphically evaluating the efficacy of our model structure, assumptions and parameter values.

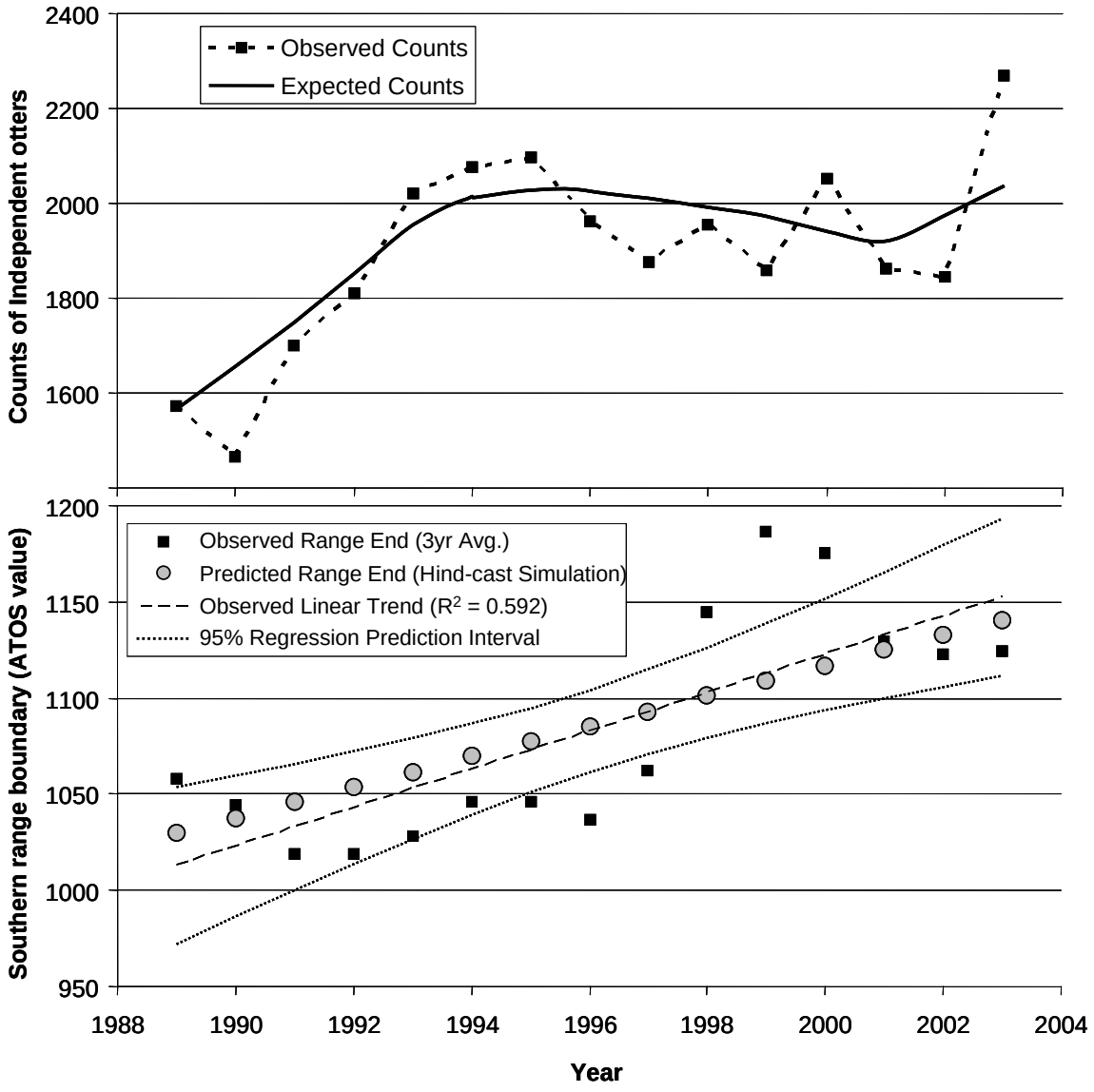

Figure 36. Results of a historical simulation of population dynamics for the southern sea otter population over the years 1989–2003. Predicted population counts, based on the simulation, are shown at top, with observed counts for comparison. Predicted range expansion to the south (increasing ATOS values over time) is shown at bottom, with observed range-end boundaries shown for comparison. The range end was defined as the point along the coast at which 99.75% of the sea otter population was to the north, based on the annual spring survey. A linear least-squares curve was fit to the observed range-end dataset, and is plotted (along with the 95% prediction interval) to illustrate the correspondence between the predicted and observed mean rate of expansion.

We conducted forward simulations in a similar way, projecting 15 years of population dynamics and range expansion using matrix multiplication. We first created 500 unique dispersal kernels by randomly selecting stage- and location-specific Laplace distribution parameters ($\sigma_{i,x}$) from within the ranges listed in Table 10. For each of the resulting 500 movement matrices, we ran 20 simulations using different demographic matrices: the first 10 iterations were parameterized using the best-fit maximum likelihood values from 1992-2001

(Chapter 2; Table 10, estimates 1–10), while for iterations 11–20 we randomly selected vital rates from within the 80% confidence intervals associated with mark-recapture parameter estimates (Chapter 2; Table 10, estimates 10–11). Confidence intervals for each estimate were calculated from standard errors using a logit-based "back transform" method (Burnham and Anderson 1998). The random combinations of dispersal and demographic estimates resulted in 10,000 unique iterations of the simulation model.

We summarized simulation results graphically by plotting frequency histograms of three key results: the predicted number of independent otters south of Pt. Conception (i.e. in sub-population 6) after 10 years, the predicted number after 15 years, and the predicted rate of range expansion to the south (in units of km/year). We estimated the mean, median, mode and variance for these three variables, as well as their 95% confidence limits. To calculate confidence intervals we assumed a negative binomial probability distribution in the case of the number of otters south of Pt. Conception, and a Weibull probability distribution in the case of the range expansion speed. We also estimated summary statistics for the net population growth rate (λ, calculated as the geometric mean rate of growth for each simulation), which was normally distributed.

Finally, we calculated the sensitivity of simulation results to all model parameters using multiple regression analysis: specifically, we calculated the proportion of variance in three response variables (the predicted number of otters south of Pt. Conception after 15 years, the rate of southward range expansion, and λ) explained by each of the demographic and dispersal parameters, after accounting for variance due to all other parameters. Individual variance components were estimated by their partial coefficients of determination (r^2_p), following (Neter et al. 1990).

Results

The historical projection simulation resulted in population dynamics that were consistent with observed survey counts over the same period (Figure 36a). While this was not especially surprising (the survey counts were one of the data sets used to fit the demographic rates, along with carcass data), it nonetheless suggested that the resulting stage distribution vector for 2003 was reasonably accurate, and also clearly demonstrates the range of different growth rates possible under the simulation parameters. Also encouraging was the close agreement between actual southward range expansion over the past 15 years and the predicted population wave speed. Although the position of the southern range boundary from year-to-year was highly variable, the long-term trend was fit by a linear expansion rate of approximately 4.9 km/year ($R^2 = 0.59$). The mean predicted rate of expansion over the same period, as calculated from stage-specific dispersal and demographic rates, was 3.95, a value not significantly different from the observed trend (Figure 36b).

The net annual rate of population increase (λ) for all forward simulations was 1.01, and 95% of the simulations resulted in $\lambda$of 0.971–1.052. The rate of population growth to the south of Pt. Conception surpassed that of the rest of the population in almost all instances, with 95% of the simulations showing a rate of increase south of Pt. Conception of 4–20% per year.

The median number of independent otters south of Pt. Conception after 10 years was 117, and after 15 years this value had increased to 131 (Figure 37). The rapid growth to the south was partly attributable to dispersal from other portions of the population, but also reflected a high intrinsic rate of growth. The interaction between dispersal and intrinsic population increase resulted in continued range expansion to the south in virtually all simulations: the median predicted wave speed was 4.9 km/year over the 15 year projection (Figure 38). Interestingly, this wave speed is precisely the same as the average rate of expansion over the past 15 years (Figure 36). Continued range expansion at this median rate would mean that after 10 years the southern range boundary will have moved to a location near Santa Barbara harbor mouth (ATOS = 1267), and after 15 years to Carpinteria (ATOS = 1316). There is a great deal of uncertainty around these estimates: the 95% confidence interval for the 15 year estimate was ATOS = 1183–1584. Table 11 summarizes all simulation statistics.

Table 11. Summary of results from simulations

Variable	Mean	Std. dev.	Median	Mode	L95	U95
Net rate of increase (λ)	1.011	0.021	1.012	1.01	0.971	1.052
S. of Pt. Conception, 10yrs	120.69	38.477	117	107	57	207
S. of Pt. Conception, 15yrs	136.63	53.212	131	121	53	259
Southern Exp. Speed(km/yr)	5.0679	3.3469	4.86	1.43	0.422	13.82
Range End, 10 yrs	1271		1267	1199	1178	1446
Range End, 15 yrs	1322		1316	1213	1183	1584

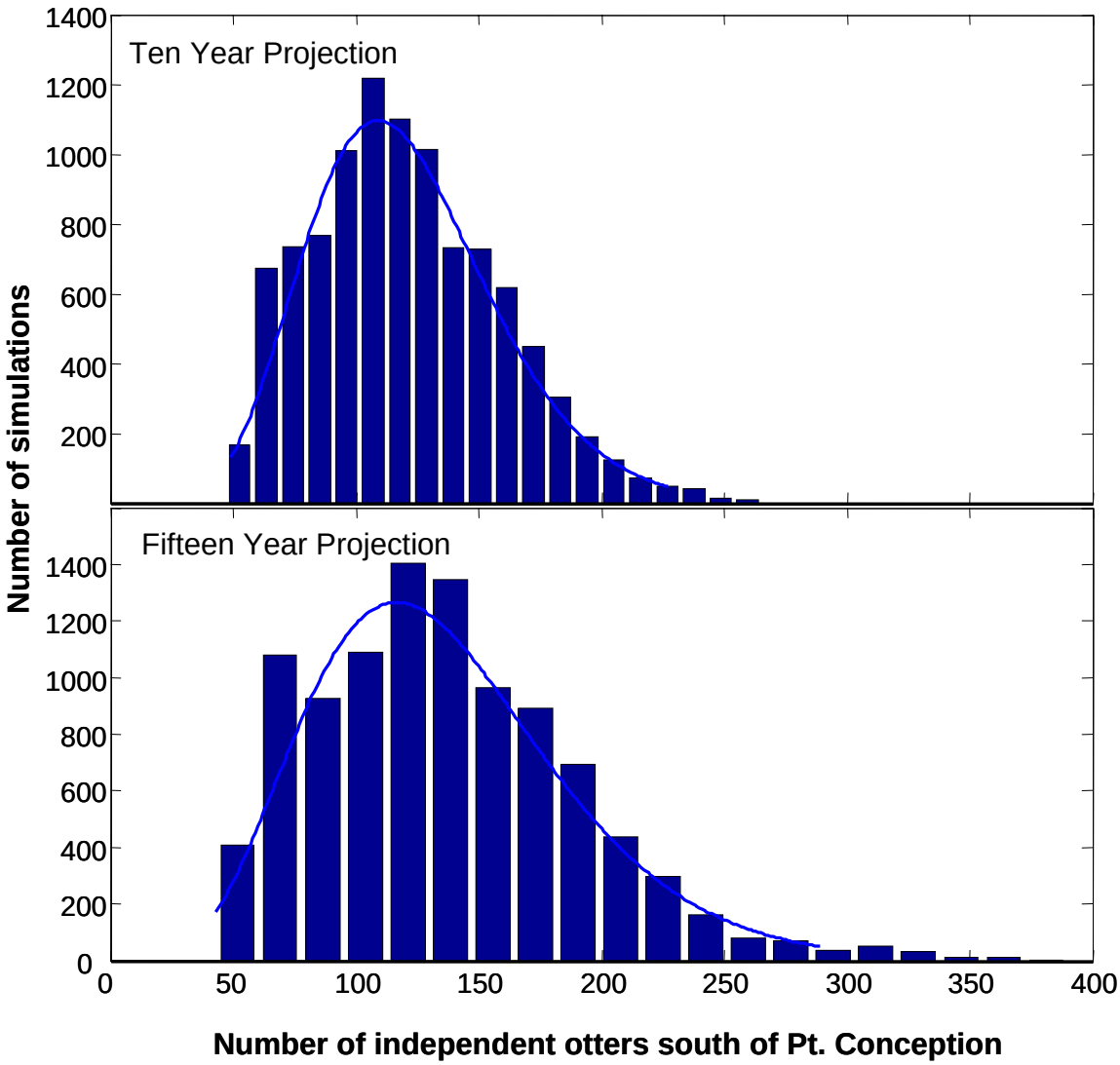

Figure 37. A frequency distribution of predicted outcomes is shown for two of the key simulation results: the expected number of independent sea otters south of Pt. Conception after 10 years (top) and after 15 years (bottom). The distributions were well described by negative-binomial probability distributions.

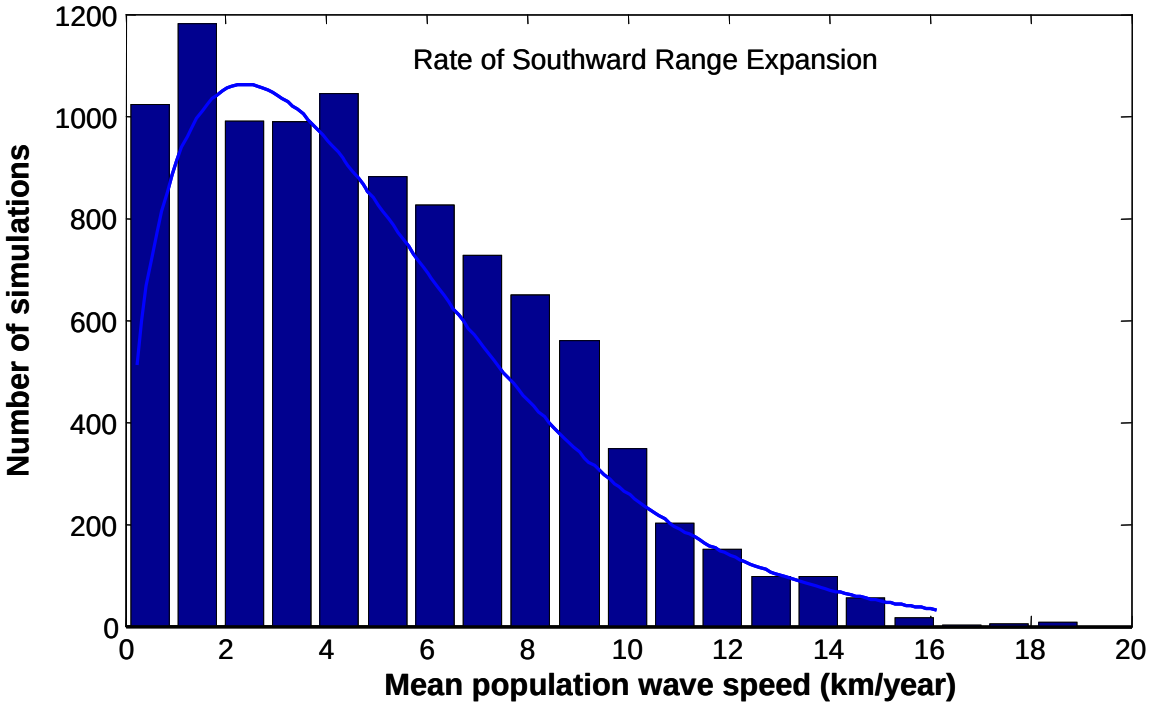

Figure 38. A frequency distribution of the predicted rate of southward range expansion is shown, based on the results of 10,000 replicate simulations. A weibull probability distribution was fit to the raw data.

The simulation results were sensitive to both variation in dispersal and variation in survival parameters, but the relative magnitude of sensitivities was quite different for different response variables. Variation in dispersal parameters had the most substantial impact on the predicted number of individuals south of Pt. Conception, but had a negligible effect on net population growth (Figure 39). Not surprisingly, variation in survival rate parameters at the south end of the range had a strong effect on all three response variables; however, while variation in survival rates at the center of the range had minimal effect on future range expansion and population growth south of Pt. Conception, their impact on net population growth was three times greater than survival rates at the south end of the range (Figure 39).

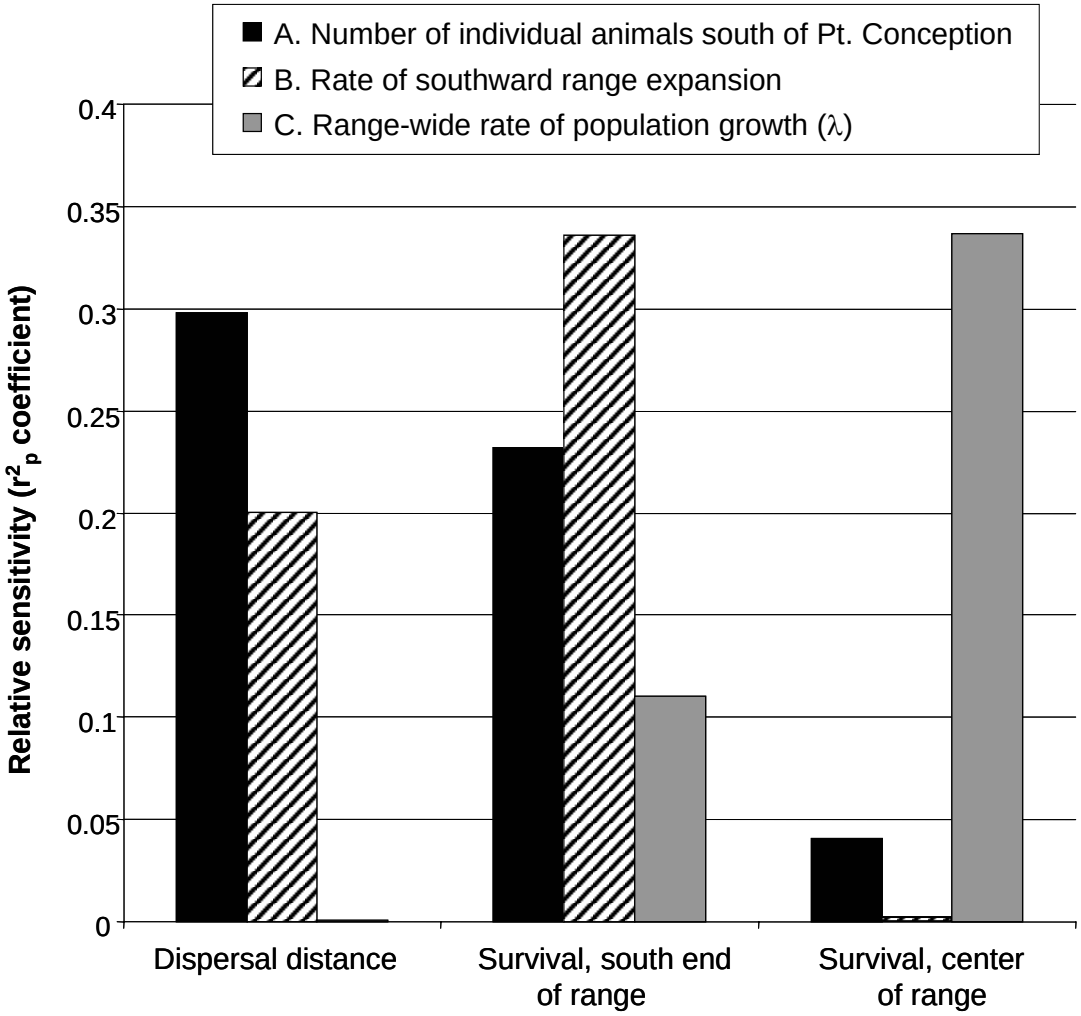

Figure 39. Results of a sensitivity analysis, showing the relative proportion of the variance in simulation dynamics explained by three groups of model parameters: dispersal rates, survival rates at the south of the range (sub-populations 5 and 6) and survival rates at the center of the range (sub-populations 3 and 4). Sensitivities are shown for three response variables: A) the number of individual otters south of pt. conception after 15 years, B) average southward wave speed, or rate of range expansion to the south, and C) the overall rate of population increase over the simulation period.

A closer inspection of stage-specific sensitivities showed that, in terms of dispersal, juvenile/sub-adult female movement rates had the greatest effect on population growth and range expansion to the south (Figure 40). Dispersal of Juvenile/Sub-adult males had a significant effect on the expected number of individuals south of Pt. Conception, but virtually no effect on the rate of southward range expansion. Adult male dispersal had almost no effect on the simulation results, despite the long-distance movements frequently conducted by this class of animals. Stage-specific survival rates showed a similar pattern of sensitivities: variation in sub-adult female survival had the greatest impact on simulation results, while juvenile and adult female survival had less of an effect (Figure 41). The only result showing any sensitivity to male survival rates was the number of otters south of Pt.

Conception, and variation in male survival had almost no effect on the rate of range expansion or on net population growth.

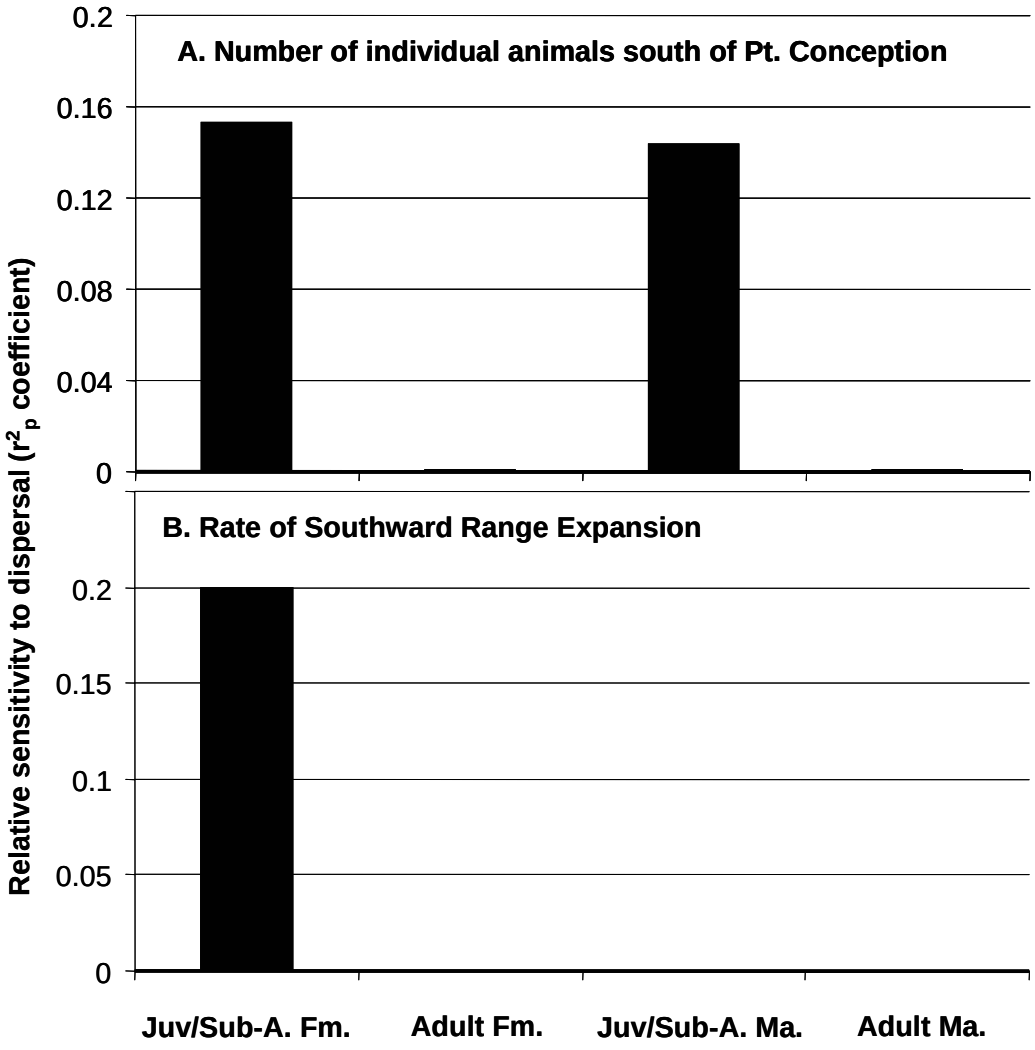

Figure 40. Results of a sensitivity analysis of dispersal parameters, showing the relative proportion of the variance in simulation dynamics explained by stage- and sex-specific dispersal rates. Sensitivities are shown for two response variables: A) the number of individual otters south of pt. conception after 15 years, B) average southward wave speed, or rate of range expansion to the south.

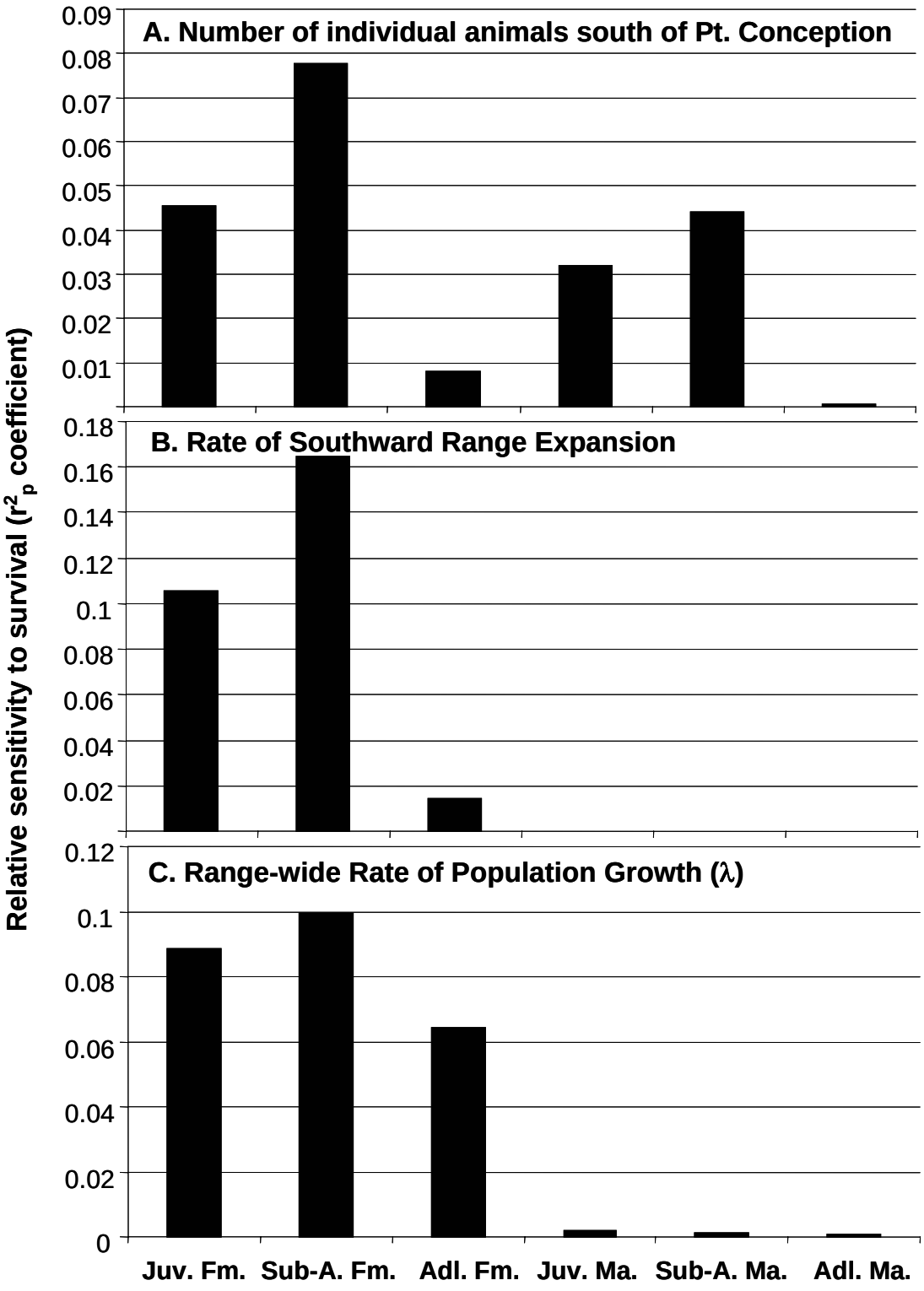

Figure 41. Results of a sensitivity analysis of survival parameters, showing the relative proportion of the variance in simulation dynamics explained by stage- and sex-specific survival rates. Sensitivities are shown for three response variables: A) the number of individual otters south of pt. conception after 15 years, B) average southward wave speed, or rate of range expansion to the south, and C) the overall rate of population increase over the simulation period.

Discussion

The predictions of our hind-cast model closely matched the historical data on rates of southward range expansion, suggesting that estimation of asymptotic wave speed (Neubert and Caswell 2000) is an appropriate technique for simulating range expansion of southern sea otters. This method is particularly appropriate for a population that is expanding along a 1-dimensional axis, as is the case with the southern sea otter. Because it incorporates information on stage-specific dispersal probabilities, demographic rates and population structure, the integrodifference approach is also likely to provide a better approximation to range expansion dynamics than the 1-dimensional diffusion model used previously to model invasion speed in sea otters (Lubina and Levin 1988).

Explicit analysis of uncertainty can provide useful insights to managers (Doak and Mills 1994, Pascual and Adkison 1994, Ralls and Taylor 2000). The best way to incorporate uncertainty into management decisions is to consider, as in our analysis, the full range of expected outcomes (Gerber et al. 2004). Projections of both the number of independent otters at Point Conception and the rate of southward range expansion were highly variable, reflecting the uncertainty in input parameter estimates and uncertainty about the ultimate causes of fluctuations in survival rates, such as density dependence, disease, and fishing interactions.

Despite this variability, sensitivity analysis of the model's predictions gave us a greatly improved understanding of the processes underlying population growth and range expansion. Sensitivity analysis in this case serves two main purposes. First, it identifies the parameters to which the model is most sensitive: better estimates of these parameters will therefore do most to improve the precision of the model predictions. Our analysis identified the survival rate of juvenile and sub-adult females at the end of range as a key parameter influencing both population growth and range expansion to the south of Pt. Conception. Hence, fieldwork designed to improve estimates of survival rates of young females in southern areas would do most to reduce uncertainty in these particular predictions.

Second, sensitivity analysis highlights the particular components of the population that are driving range expansion and/or population growth. These results are sometimes not intuitively obvious. For example, although males are more likely to move long distances than females and most of the individuals that travel south of Point Conception are males, male movements proved much less important than female movements (Figure 40). Movement rates of juvenile and sub-adult females had the greatest effect on both population growth and range expansion to south, whereas dispersal of their male counterparts had no impact on the rate of southward range expansion, and variation in adult male survival had almost no effect on either population growth or range expansion. This last result is not so surprising considering that range expansion by males alone would provide no intrinsic population growth (i.e. reproduction) at the ends of the range: because reproduction is ultimately what drives population growth and subsequent range expansion, it is the movement and survival of females that is the limiting factor for both processes. This method of sensitivity analysis also allows for evaluation of spatial patterns: for instance, female survival at the center of the range probably has little effect on the rate of range expansion,

but is the most important demographic parameter for predicting growth of the population as a whole (Figure 39).

Our simple multi-state matrix model does not explicitly account for a variety of important aspects of sea otter biology and ecology: these include density dependence (Laidre et al. 2001), spatial and temporal variation in habitat quality (Doak 1995, Thomas and Kunin 1999, Virgl and Messier 2000), responses to ephemeral phenomenon such as episodic prey recruitment events (Watt et al. 2000), seasonal reproductive peaks and movement patterns (Jameson 1989), and important behavioral characteristics such as dietary specializations (Estes et al. 2003b), territoriality (Jameson 1989), contagious distribution, and male/female (or age class) segregation at smaller spatial scales. It is worth noting that the model actually does implicitly account for some of these factors (such as density dependence and habitat quality), in so far as these factors have affected past and present vital rates and movement probabilities within the existing range.

Despite the above-mentioned limitations, our model provides a robust and generalizable approach to understanding and predicting population dynamics in southern sea otters by making use of all existing demographic and dispersal data. It represents a unique synthesis of a multi-state dispersal matrix and the integrodifference equation approach to calculating invasion speed. Our model should provide a useful and flexible tool for conservation biologists and managers, and can be easily expanded upon or improved as additional data and more precise parameter estimates for southern sea otters become available.

Chapter 5. Foraging Ecology

M. Tim Tinker, James A. Estes, Michelle Staedler, James L. Bodkin

Abstract

1. Longitudinal foraging data collected from 60 sea otters implanted with VHF radio transmitters at two study sites in Central California over a three-year period demonstrated even greater individual dietary specialization than in previous studies, with only 54% dietary overlap between individuals and the population.
2. Multivariate statistical analyses indicated that individual diets could be grouped into three general "diet types" representing distinct foraging specializations. Type 1 specialists consumed large size prey but had low dive efficiency, Type 2 specialists consumed small to medium size prey with high dive efficiency, and Type 3 specialists consumed very small prey (mainly snails) with very high dive efficiency.
3. The mean rate of energy gain for the population as a whole was low when compared to other sea otter populations in Alaska but showed a high degree of within- and between-individual variation, much of which was accounted for by the three foraging strategies. Type 1 specialists had the highest mean energy gain but also the highest within-individual variance in energy gain. Type 2 specialists had the lowest mean energy gain but also the lowest variance. Type 3 specialists had an intermediate mean and variance. All three strategies resulted in very similar probabilities of exceeding a critical rate of energy gain on any given day.
4. Correlational selection may help maintain multiple foraging strategies in the population: a fitness surface (using mean rate of energy gain as a proxy for fitness) fit to the first two principal components of foraging behavior suggested that the three foraging strategies occupy separate fitness peaks.
5. Food limitation is likely an important ultimate factor restricting population growth in the center of the population's range in California, although the existence of alternative foraging strategies results in different impacts of food limitation on individuals and thus may obscure expected patterns of density dependence.

Introduction

Intraspecific variation in diet and foraging behavioral strategies is characteristic of many animal populations (Partridge and Green 1985, Bolnick et al. 2003). There is also both theoretical (Glasser 1982) and empirical evidence (e.g. Schindler et al. 1997) to suggest that the degree of individual specialization increases as forager populations become food-limited at high densities, and when intraspecific competition exceeds interspecific competition (Smith and Skúlason 1996). Thus, patterns of variation in diet and foraging success are important to measure if we are to fully understand the role of food-limitation in regulating predator populations. Characterizing the sources of variation in diet – individual, spatial and temporal – also can help to clarify the relationships between foraging ecology and population dynamics (Partridge and Green 1985).

Homeothermic vertebrates that dive to obtain their food provide excellent examples of energy-limited predators, and a number of recent studies have used diving birds and mammals to test predictions of foraging theory (Ball 1994, Wilson et al. 1996, Boyd et al. 1997, Mori 1998). Due to high metabolic demands of a marine existence (Costa and Kooyman 1982, Adams et al. 1991, Croll and McLaren 1993) and the often unpredictable or patchy distribution of their prey resources, the fitness of many marine diving birds and mammals is strongly tied to foraging efficiency and energy acquisition rates (Croxall et al. 1988, Costa et al. 1989, Doidge and Croxall 1989, Wanless et al. 1995). A number of these species exhibit individually variable foraging strategies, including herring gulls (Pierotti and Annett 1991), northern fur seals (Gentry et al. 1986, Loughlin et al. 1987, Costa 1988) and sea otters (Estes et al. 2003b).

Sea otters provide a particularly good model for investigating variation in foraging behavior because their distribution is limited to the near-shore marine habitat where they are easily observed and they bring all captured prey to the surface to handle and consume: it is thus possible to study their diet and foraging behavior non-invasively through observational studies (e.g. Estes et al. 1981, Kvitek et al. 1993, Doroff and Degange 1994, Mathews 1996, Jolly 1997). Sea otters also utilize a variety of different habitat types, and occur at varying population densities throughout their range, facilitating comparative studies of the effects of habitat and population status on foraging behavior (Estes et al. 1982, Estes 1990, Dean et al. 2002).

The southern sea otter (*Enhydra lutris nereis*) feeds entirely on sub-tidal and inter-tidal invertebrates (Riedman and Estes 1990) and has a highly diverse and individually variable diet (e.g. Ostfeld 1982, Kvitek and Oliver 1988, Lyons 1991, Estes et al. 2003b). Sea otters have high metabolic rates and can consume 25% or more of their own body weight each day (Costa 1978) resulting a tendency to limit the abundance of their primary prey populations, a trait which has important consequences for community structure (Estes and Palmisano 1974, Estes et al. 1982). Foraging effort increases and energy acquisition rates decrease as sea otter populations reach equilibrium densities (Estes et al. 1982, Estes et al. 1986, Garshelis et al. 1986, Watt et al. 2000, Dean et al. 2002, Gelatt et al. 2002).

We investigated the diet and foraging behavior of southern sea otters in central California in order to characterize patterns of variation and evaluate the implications for individual fitness.

We collected longitudinal observational data from marked study animals over a 3 year period at two locations where otter densities were relatively high and temporally stable (or decreasing slightly). Our objectives were threefold: first, we sought to measure the degree of individual specialization in diet, to determine whether there are consistent and distinct modes of prey selection and foraging behavior in southern sea otters and, if so, whether these strategies vary spatially or between sex classes. Our second goal was to measure variation in the rate of energy gain for individual otters, examine the relationship between foraging success and individual fitness, and evaluate the hypothesis that otters are food-limited in the center of their range. Finally, we wished to describe the interrelationships between foraging strategy and foraging success. Specifically, we sought to compare the rate of energy gain between different strategies and evaluate the fitness surface formed by plotting energy gain as a function of foraging behavior (Sinervo and Svensson 2002).

Methods

Data Collection

All foraging data were collected between January 2001 and April 2004 from sea otters that were tagged and instrumented with radio transmitters (see Chapter 1). Because very few foraging observations were obtained from animals captured near Pt. Conception, we limit consideration here to those captured in the Piedras Blancas- Simeon area (Site 1) and in the Monterey Bay area (Site 2 (Monterey; Figure 42).

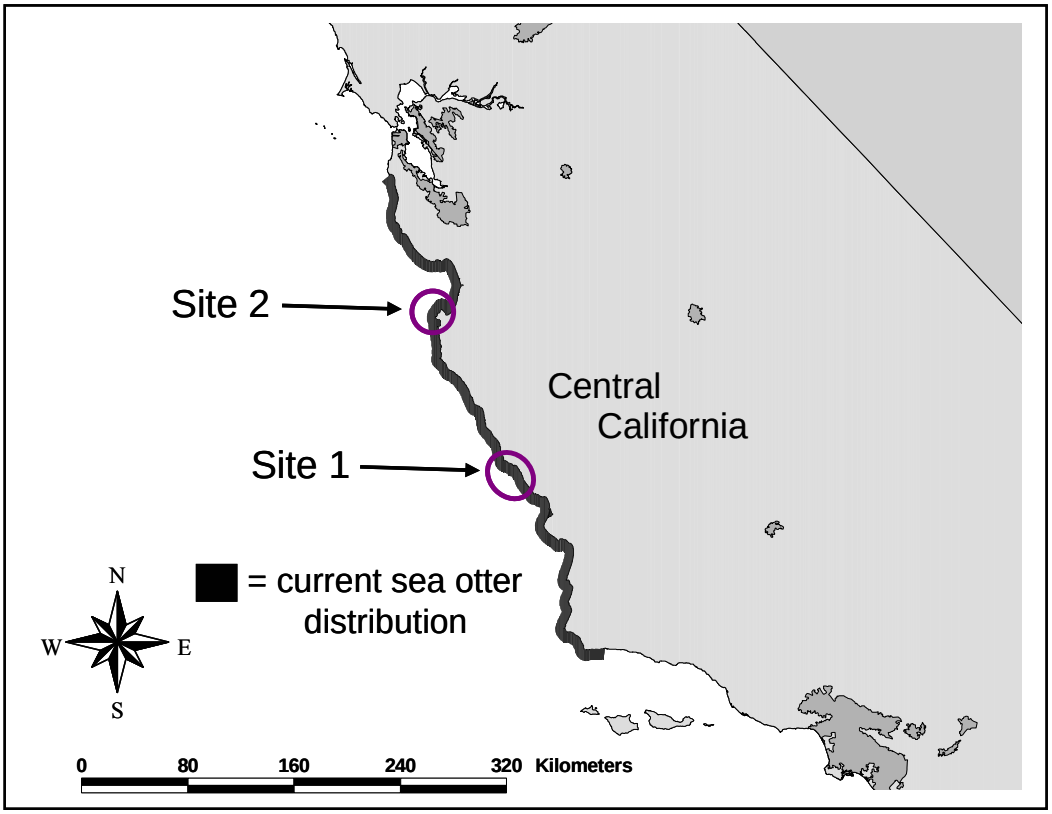

Figure 42. Map of the central California showing the current distribution of the sea otter (Enhydra lutris nereis) and the locations of the two study sites.

Capture and tagging activities were conducted intermittently throughout the study period, resulting in a gradually increasing sample size (Table 12). Study animals were captured by scuba divers using re-breather equipment and "Wilson Traps" (McCleneghan and Ames 1976). Captured animals were transported to a shore-based veterinary mobile laboratory where they were immobilized using standard anesthetic techniques (Monson et al. 2001), equipped with flipper tags (using unique tag-color combinations for visual identification at distance) and instrumented with an abdominally-implanted VHF transmitter (Williams and Siniff 1983). A series of standardized measurements were collected, including weight, length, girth, tooth condition and age estimate. Otters were revived post-surgery using a reversal agent (Monson et al. 2001), transported back to their capture location and released. A total of 117 sea otters were captured and instrumented as part of the larger population study, but many of these animals died or moved to inaccessible regions along the coast before adequate samples of foraging data could be collected. Consequently, we restrict all analyses to the 60 animals from which a reasonable quantity of foraging data (≥10 foraging bouts and ≥ 300 feeding dives per animal) were collected (Table 12).

Table 12. Sample sizes used for analyses of foraging data. New study animals added to the sample each year are summarized by sex (at least one full year of data were collected for each animal, and for most individuals 2–3 years of data were collected, unless the animal died before the end of the study). Also shown are the number of foraging bouts and feeding dives recorded for all study animals during each year.

		Study Animals Captured		Number of	Number of
Study Site	Year	Females	Males	bouts observed	dives recorded
1. San Simeon	2001	9	3	196	10778
	2002	18	5	209	10244
	2003	0	0	298	12231
	2004	0	0	24	937
	sub-total:	*27*	*8*	*727*	*34190*
2. Monterey	2001	5	1	25	1641
	2002	2	0	105	4484
	2003	14	3	113	5169
	2004	0	0	62	2568
	sub-total:	*21*	*4*	*305*	*13862*
	Total:	48	12	1032	48052

We systematically collected observational foraging data from tagged and instrumented otters using standard protocols (Ralls et al. 1995, Watt et al. 2000, Estes et al. 2003b). Field observations were collected 3-7 days per week throughout the study period, and two sampling methods were used. The first method involved teams of 1–2 observers making systematic searches of the study areas and sequentially targeting specific animals for foraging observations.

The second method involved 24-hour, focal-animal observations of a single study animal, during which time all daylight foraging behavior was recorded. The 24-hour sessions also allowed me to quantify individual activity budgets, in particular the percent of time spent feeding (Ralls and Siniff 1990). In both sampling methods, otters were initially located by

radio signal using standard telemetric techniques and then visually monitored them from shore using a 30× spotting scope (Questar Inc., Isanti, MN). Foraging bouts (defined as unbroken sequences of feeding dives) typically lasted 1-4 hours, and data were recorded throughout the entire bout or for as many dives as possible. The information recorded included date and time, precise location of each dive (determined by visual triangulation using GPS, compass and laser range-finder), duration of the subsurface dive interval (" DT") and the post-dive surface interval ("ST") for each feeding dive (in seconds), success of each dive (i.e. whether or not prey was captured), species of prey captured, number and size of prey items, handling time per prey item, tool use, and ambient conditions (including sea-state, wind, etc.). Prey size was recorded as the estimated diameter of the shell or maximum body dimension (excluding appendages), categorized into 5 cm size-classes. For many observations, prey could not be identified to species; in such cases we classified prey to the lowest possible taxonomic unit, and we listed as "unknown" any prey items that could not be reliably categorized. Any prey items that were stolen by or from the focal animal were also recorded (and in the case of females with dependant pups, the number of items that were shared with the pups).

Foraging bouts represent the smallest functional sampling unit for statistical analyses: all data were collected on a per-dive basis, but then tallied to derive per-bout measurements (mean dive/surface durations, success rate, frequency of prey types, etc.). Every attempt was made to achieve balanced sample sizes for each study animal in all seasons and throughout each animal's particular home range. The 24-hour, focal-animal sessions helped account for potential biases due to time of day or feeding location, because the focal animal was followed throughout its daily movements during these sessions. A few study animals tended to spend considerable time feeding far from shore, or in areas that were difficult or impossible to view from shore (e.g. private property): in order to avoid bias due to feeding location, we augmented the shore-based observations for these animals with boat-based observations, using a 17 foot skiff. In the case of boat-based observations we used 12× image-stabilized binoculars to view the otters, but all other methods were identical to shore-based observations.

Data Analysis

We calculated two indices of diet composition: the relative frequency of occurrence of each prey type, and the biomass contribution of each prey type to the diet. The first index was calculated as the proportion of all recorded prey captures comprised by each prey type, and provided a measure of the likelihood of observing a particular prey species at a given place and time. We used this index to evaluate spatial and temporal differences in diet composition at the level of the population. To evaluate seasonal variation, we tested for an interaction between month and prey type. To evaluate spatial variation we tested for an interaction between study site and prey type. In both cases a chi-square contingency test was used to assess the significance of the interaction.

The second index of diet composition, prevalence of each prey type by biomass, accounts for the number of items per dive and the size of each item, and the frequency of occurrence. The diameter of each prey item was converted into an estimate of wet edible biomass (*m*)

using functional relationships between wet-weight and diameter from the literature (see Appendix A). For each successful dive that was observed (j=1,2…J), let $n_{i,j}$ and $m_{i,j}$ represent the number of items and the per-item biomass, respectively, for prey of type i ($n_{i,j}$ = $m_{i,j}$ = 0 for all prey types except those actually captured on dive j). We calculated p_i, the proportion of the diet (in terms of biomass) comprised by prey type i, as:

$$p_i = \frac{\sum_j n_{i,j} m_{i,j}}{\sum_i \sum_j n_{i,j} m_{i,j}} \qquad 39$$

Equation 39 was solved for the population as a whole, and then separately for each study animal, such that $p_{i,k}$ represents the prevalence of prey type i in the diet of otter k. If individuals do not differ significantly with respect to diet, then the diet composition of each individual would essentially overlap with the population-level diet ($p_{i,k} \cong p_i$). Conversely, if $p_{i,k} \neq p_i$ then individual diets must vary: this appears to be the case for sea otters, based on previous reports (Riedman and Estes 1990, Estes et al. 2003b). In order to measure the degree of individual specialization in the current sample, we calculated a "proportional similarity" index (PS_k) for each otter:

$$PS_k = \sum_i \min\left(\frac{p_{i,k}}{\sum_i p_{i,k}}, \frac{\sum_k p_{i,k}}{\sum_k \sum_i p_{i,k}} \right) \qquad 40$$

PS_k is the individual-equivalent to community measures of niche width (Feinsinger et al. 1981): PS_k will approach 1 for a dietary generalist, while values of $PS_k < 1$ indicate specialization on a sub-set of the population diet (Bolnick et al. 2002). We averaged PS_k across all individuals to calculate *PSI*, the proportional similarity index of the population: *PSI* represents a measure of the degree of specialization in the population as a whole. We contrasted *PSI* between study sites using single factor ANOVA.

The *PSI* value indicates the degree of individual specialization, but fails to describe the nature of the variation in individual diets. For a hypothetical population in which *PSI* = 0.5, we know that the diet of a typical individual overlaps with the population diet by only 50%; however, we do not know if each individual has a unique dietary configuration, or if there are just a few alternate dietary configurations distributed evenly among individuals. To distinguish between these alternate scenarios of individual variation, we used a combination of cluster analysis and discriminant analysis to test for consistent, distinct categories of diet composition.

To simplify interpretation of results, we combined similar prey species together to form 13 exhaustive prey categories (Table 13). The raw data analyzed were $p_{i,k}$, the prevalence (by mass) of prey type i in the diet of individual k: thus individual otters represent sample units (N = 60) and prey types represent the variables of interest. We used hierarchical cluster analysis to detect discontinuous groupings or "clumps" of data points in multidimensional space (McGarigal et al. 2000). The distance measure used was the square of the Pearson

product-moment correlation (r^2), as this measure maximized the cophenetic correlation coefficient and thus most faithfully represented the structure of the raw data (Gauch 1982). We used Ward's minimum variance method to link similar points, and the number of significant clusters was determined by graphical examination of the resulting dendrogram and scree plot of inter-cluster distance vs. number of clusters (McGarigal et al. 2000). After classifying each otter by cluster membership, we used discriminant analysis to evaluate the effectiveness of the classification (the frequency with which otters were correctly assigned cluster membership, using a "jack-knife" re-sampling test procedure) and to determine the key prey variables that contributed most to the classification.

Assuming that distinct clusters could be identified, they were described in terms of the relative frequency of key prey types. We compared *PSI* values among diet types using single-factor ANOVA, to determine whether the degree of prey specialization differed between diet types. We used a log-linear model to evaluate the interactions between diet type, study site and sex, testing the null hypothesis that diet types were equally distributed among sexes and study sites. The best-fit model was selected by minimizing the Bayesian Information Criterion, or *BIC* (Hilborn and Mangel 1997).

Table 13. Summary of diet composition of sea otters at two study sites, showing the frequency of occurrence of prey types on foraging dives (prey comprising ≤ 0.1% of occurrences are not shown). For prey that could not be identified to species, the lowest-possible taxonomic identification is shown. Prey types are classified into one of 13 categories for use in multivariate analyses (see text for details).

Common Name	Latin Name or Taxonomic group	Prey Type category	% at Site 1	% at Site 2
kelp crab	*Pugettia producta (*and *richii)*	kelp crab	20.05	8.40
turban snail	*Tegula spp.*	snail	10.97	17.30
mussel	*Mytilus californianus*	mussel	8.51	17.76
purple urchin	*Strongylocentrotus purpuratus*	urchin	9.11	16.11
clam, unidentified species	various pelecypod species	clam	14.25	10.57
cancer crab	*Cancer spp.*	cancer crab	10.43	9.00
crab, unidentified species	various decapod species	crab (un-id)	8.89	5.97
Fat innkeeper worm	*Urechis caupo*	worm	3.38	4.60
small kelp fauna	various small invertebrates	other (rock)	7.20	0.22
Sea star	*Pisaster sp.*	sea star	3.94	0.82
sand crab	*Emerita analoga, Blepharipoda occidentalis*	other (sand)	0.42	2.09
sand dollar	*Dendraster excentricus*	other (sand)	0.91	1.58
abalone	*Haliotis spp.*	abalone	0.54	1.94
octopus	*Octopus sp.*	cephalapod	0.36	0.71
worm, unidentified species	various annelid species	worm	0.21	0.72
chiton	*Mopalia sp., Tonicella sp.*	other (rock)	0.07	0.58
limpet	*Diodora aspera*	other (rock)	0.01	0.39
scallop	*Hinnites multirugosus*	clam	0.11	0.21
cockle	*Clinocardium nuttallii*	clam	0.01	0.28
gaper clam	*Tresus nuttallii*	clam	0.24	0.03
sea cucumber	various holothurian species	other (rock)	0.09	0.17
red urchin	*Strongylocentrotus franciscanus*	urchin	0.02	0.21
squid	*Loligo opalescens*	cephalapod	0.06	0.12
isopod	various isopod species	other (rock)	0.13	0.01

Differences in diet composition could potentially be associated with differences in the diving and feeding behavior of alternative specialists. However, evaluating trends in diving/feeding behavior is complicated by the large number of behavioral variables that we measured. We used principal components analysis (PCA) to reduce the number of variables needed to describe behavior: this analysis collapsed many behavioral variables into a few dominant, orthogonal axes that were used for further tests. Individual otters were used as sample units, and the variables of interest were mean DT, mean ST, variation in ST, dive success rate (the proportion of dives in which prey were captured), the "surface duration ratio" or SDR (defined as the ratio of ST for successful dives: ST for unsuccessful dives), the average number of prey items captured on a successful dive, and the mean handling time required per prey item. The principal component eigenvalues were converted to estimates of relative percent variance, and we retained the sub-set of factors explaining at least 80% of the variation in the data. These factors were then interpreted based on the component loadings of the underlying variables (McGarigal et al. 2000).

We analyzed patterns of variation in the PCA factor scores to test for differences in foraging behavior attributable to study site, sex, and diet type. We used mixed-model ANOVA to test the significance of main effects (sex was treated as a fixed effect, study site and diet type were treated as random effects) and interactions (sex–diet type and study site–diet type). We repeated the analysis for each PCA factor, and used Bonferoni-adjusted probabilities (P_{adj}) to account for the increased type-I error rate due to multiple tests. We also wished to compare the relative proportion of variation in behavior that was explained by differences between diet types, differences between individuals, and within-individual variation. Accordingly, we repeated the PCA analysis described above, but used individual foraging bouts as the sample unit. We then used random-effects, nested ANOVA to measure variation associated with diet type, individuals (nested within diet types) and foraging bouts (within-individual variation). Variance components were calculated using standard methods (Neter et al. 1990), and the analysis was repeated for each PCA factor. Estimates of percent variance explained were then calculated as the weighted means of the variance components for all PCA factors, using the factor eigenvalues as a weighting variable.

We used energy acquisition rate as an index of foraging success, and as with previous analyses of sea otter prey consumption rates (Ebert 1968, Costa 1978, Garshelis et al. 1986, Doroff and Degange 1994, Mathews 1996, Jolly 1997, Dean et al. 2002), we estimated the rate of energy gain based on observational foraging data. The simplest and most commonly used method for estimating the rate of energy gain is to calculate, for each prey type, the product of the following four variables: 1) dive success rate (excluding dives of unknown success); 2) the proportion of successful dives in which the prey type was observed (excluding dives with unknown prey types); 3) the mean number of items of the prey type captured per dive; and 4) the mean energy content per prey item. This product is summed for all prey types in the individual's diet, and then divided by the average dive interval (DT + ST) to estimate the mean energy acquisition rate. Although this approach can provide a reasonable estimate of the long-term average rate of energy gain, there are two potential problems: first, it provides no indication of the degree of variation in the rate of energy gain. The long-term average may not provide a good measure of day-to-day success if the rate of energy gain varies greatly from bout-to-bout, or is not distributed as a normal variable (e.g. the distribution is skewed or multimodal). The second problem is one of bias: potentially

important sources of uncertainty in the raw data – dives of unknown success, dives with unknown or unrecognized prey types, dives with unknown numbers of prey items – are simply ignored under the assumption (generally untested) that unrecorded data points are well represented by recorded data points. Violations of this assumption could have significant impacts on the resulting estimates, however, because dive outcome is unknown for many dives and approximately 50–60% of recorded prey captures fall into the "unidentified" category (an unavoidable consequence of observing otters feeding on small prey at great distances). There are in fact a number of reasons to doubt the assumption that recorded data is an unbiased sample of unrecorded data: large prey species are easier to identify at distance and thus more likely to be recorded than smaller species; prey types captured on dives with short surface intervals are less likely to be recorded (such dives are often associated with small prey items); and dive success is less likely to be confirmed on dives with short surface intervals. These biases could potentially skew results, though not necessarily in predictable ways.

Both of the problems described above can be addressed by an alternative approach that directly incorporates uncertainty into the analysis. Dean et al. (2002) used a Monte Carlo re-sampling analysis to create large numbers of "simulated foraging bouts", using summary statistics from the raw data to parameterize each simulation. Their model did allow for stochastic variation in the rate of energy gain, but did not directly address the potential biases associated with unrecorded data. Here we develop a slightly different re-sampling model to analyze foraging success (rate of energy gain), explicitly accounting for uncertainty and potential biases, but using the actual data for analysis rather than simulations. The general approach is to "boot-strap" foraging bouts (draw bouts randomly with replacement) from the database for each animal, and then calculate energy gain on a dive-by-dive basis for each bout. The energy gain is summed for all the dives in the bout and then divided by the total bout duration to create an estimate of net rate of energy gain ($kJ \cdot min^{-1}$). In the case of dives with no missing information, the calculations are straightforward: the energy content of each captured prey item is estimated using species-specific, size-energy relationships (see Appendix A) and summed for the number of items of each prey type (net energy gain = 0 for unsuccessful dives). Adjustments are then made for prey sharing or stealing: any prey items shared with a pup or stolen by another otter are subtracted, while any additional prey items stolen from another otter are added.

In the case of dives with one or more unrecorded parameters (e.g. unknown dive success, unknown prey, or unknown number of items), an appropriate estimate for the parameter in question is assigned based on the characteristics of the dive. Because the post-dive surface interval (ST) is strongly correlated with dive success rate and the number/size of prey items, this information can be used to restrict the range of possible values for each unrecorded parameter. For example, dive outcome can be modeled as a binomial variable (successful = 1, unsuccessful= 0) that is a function of ST: the probability of dive success is low for dives with small ST values and high for dives with long ST values. Accordingly, for each individual otter a logit function is fit to dives with known outcome (Figure 43), and this function is used to estimate the probability of success for all dives with unknown outcome. In the case of successful dives where the prey type is known but the number of items or size of prey is unrecorded, an appropriate value is drawn (with replacement) from the observed

distributions of size class and number of items. These distributions are specific to each prey type and individual otter, and stratified by ST (short ST < 45s; medium ST ≥ 45s and < 90s; long ST ≥ 90s; this classification scheme was somewhat arbitrarily, but provided adequate sample sizes for short, medium and long surface intervals). Finally, in the case of successful dives where the prey type is unknown, the net energy gain for the dive is assigned as a random deviate from a log-normal probability distribution calculated separately for each otter and fit to the vector of estimated energy gain for successful dives with known prey types, stratified by ST.

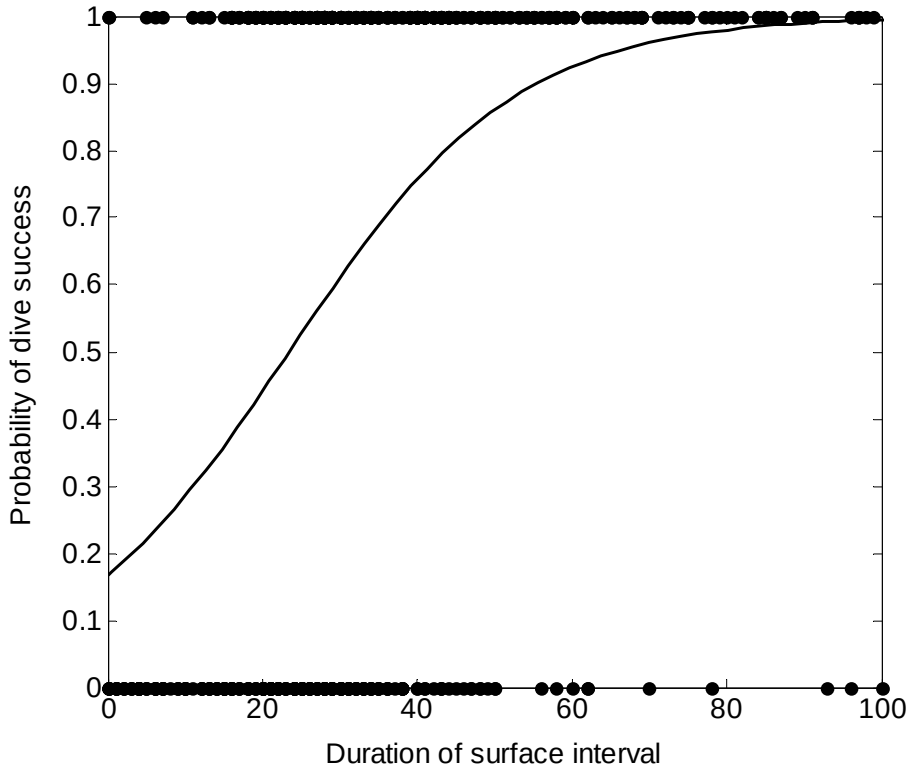

Figure 43. Sample data from one study animal illustrating the relationship between dive outcome (score of 1 = one or more prey items captured, 0 = no prey captured) and the duration of the post-dive surface interval. A logit function is fit to the data, and this function is then used to estimate the probability of dive success for dives in which the surface interval was recorded but the dive outcome was undetermined.

The boot-strap analysis described above was repeated 1000 times for each individual, to create distributions of the mean rate of energy gain (kJ per minute) and between-bout variance in the rate of energy gain. Because the model required a large database of forage data for each individual (in order to properly parameterize the various distributions), we restricted the analyses to a sub-set of the study animals for which at least 15 feeding bouts of ≥ 20 dives had been recorded. This resulted in a sample size of 39 individual otters (26 from site 1 and 13 from site 2) and a total of 629 foraging bouts consisting of 30,992 recorded dives. Two sets of analyses were conducted for adult females, one for foraging bouts recorded when the female was without a pup and one for foraging bouts recorded when the female had a dependant pup. A paired Wilcoxin signed-ranks test was used to compare the

rate of energy gain for females with vs. without a pup. The mean rate of energy gain and variance in the rate of energy gain were contrasted between study sites and diet types using two-way ANOVA. Individual rates of energy gain were found to be log-normally distributed, so all statistics were calculated using log-transformed values (therefore all contrasts made are for the geometric mean rate of energy gain).

When the average rate of energy gain during foraging bouts decreases in a population, the required foraging effort of individual otters (measured as the percent of daily activity budget spent foraging) is predicted to increase in order to meet basic metabolic maintenance requirements (Estes et al. 1986, Ralls and Siniff 1990, Gelatt et al. 2002). We calculated expected foraging effort based on the observed body weight and estimated rate of energy acquisition for each individual. We assumed that mean daily maintenance requirements were 1019 $kJ \cdot kg^{-1} \cdot day^{-1}$, the average of several published values for sea otters (Costa 1978, Costa and Kooyman 1982, Dean et al. 2002). We calculated the required total daily energy input, and divided this by the estimated rate of energy gain to obtain the expected time budget. We compared the mean expected foraging effort for females (without pups) to observed activity budgets, as recorded during 24-hour focal-animal sessions (N= 25), using a two-sample t-test.

It is generally assumed that foraging success (rate of energy gain while foraging) is important to individual survival or reproductive success; however, this is a difficult relationship to test directly because of the difficulty of measuring lifetime fitness in long-lived animals such as sea otters. Poor body condition in sea otters, indicated by a low ratio of body weight to total length, has been found to be associated with increased mortality (Bodkin et al. 2000) and lower reproductive success (Monson et al. 2000), thus body condition can be used as an indirect measure of fitness. We evaluated the importance of foraging success to individual fitness by examining the relationship between rate of energy gain and female body condition. First, we fitted a locally-weighted, least-squares regression to log-weight vs. log-length (LOWESS smoothing has the effect of relaxing assumptions of log-linearity, Green 2001), and used the residuals from this allometric relationship as an index of relative body condition (Silva 1998, Green 2001). We then used least-squares, linear regression analysis to test the relationship between body condition and the rate of energy gain while foraging (rate of energy gain was log-transformed to achieve normality).

To visualize the relationship between foraging success (net energy gain) and foraging behavior, we used Schluter and Nychka's (1994) multivariate cubic spline algorithm to fit a "fitness" surface to the principal axes of behavior. The multivariate cubic spline is a non-parametric regression technique that finds the best-fit function between a dependent variable and 2 or more independent variables. In this case the dependant variable was the standardized net rate of energy gain (w_i) for each otter, i:

$$w_i = \frac{E_i}{\overline{E}} \qquad 41$$

where E is the geometric mean rate of energy gain while foraging, minus the expected rate of energy expenditure (assuming standard field metabolic rate, Costa 1978). The independent

variables were the first two principle components of behavior (calculated using PCA: see above), with scores standardized to mean of 0 and unit variance for the sub-set of 39 study animals for which rate of energy gain was estimated. The best-fit spline function (visualized as a 3-dimensional surface) is found by adjusting the smoothing factor (λ) to minimize the GCV score (Craven and Wahba 1978). Correlational (and disruptive) selection is suggested if the resulting surface curvature results in multiple peaks (Schluter and Nychka 1994). We also used a general linear model to test for an interaction effect between the two axes of behavior. In the case of a significant interaction, we estimated the correlational selection gradient (γ) from the magnitude of the interaction coefficient (Endler 1986, Sinervo and Svensson 2002).

The type-1 error rate (α) was set to 0.05 for statistical tests, and all results are reported with appropriate test statistics and P values. In the case of non-significant test results, the power of the test to detect a "large effect" (sensu Cohen 1988), given the existing sample size and variance structure, is also reported (where power is defined as $1-\beta$, the type-II error rate). Whenever appropriate, statistics are followed (in parentheses) by ± 1 standard deviation.

Results

Based on approximately 38,500 recorded prey captures between January 2001 and April 2004, the diet of southern sea otters consisted of 24 identifiable prey types (Table 13). All 24 prey types were observed at both study sites, but the relative frequency of occurrence differed significantly ($\chi^2 = 255.6$, *d.f.* = 23, $P < 0.001$): crabs and clams occurred more frequently at site 1, while snails, urchins and mussels were more commonly observed at site 2. Diet composition also varied seasonally ($\chi^2 = 260.9$, *d.f.* = 132, $P < 0.001$), although no prevailing patterns could be discerned: rather, there were distinct seasonal peaks in occurrence whose timing differed between prey types (Figure 44). Many prey types were observed on a relatively small percentage of feeding dives, and approximately 80% of the diet at both sites consisted of the same 6 prey types (Table 13).

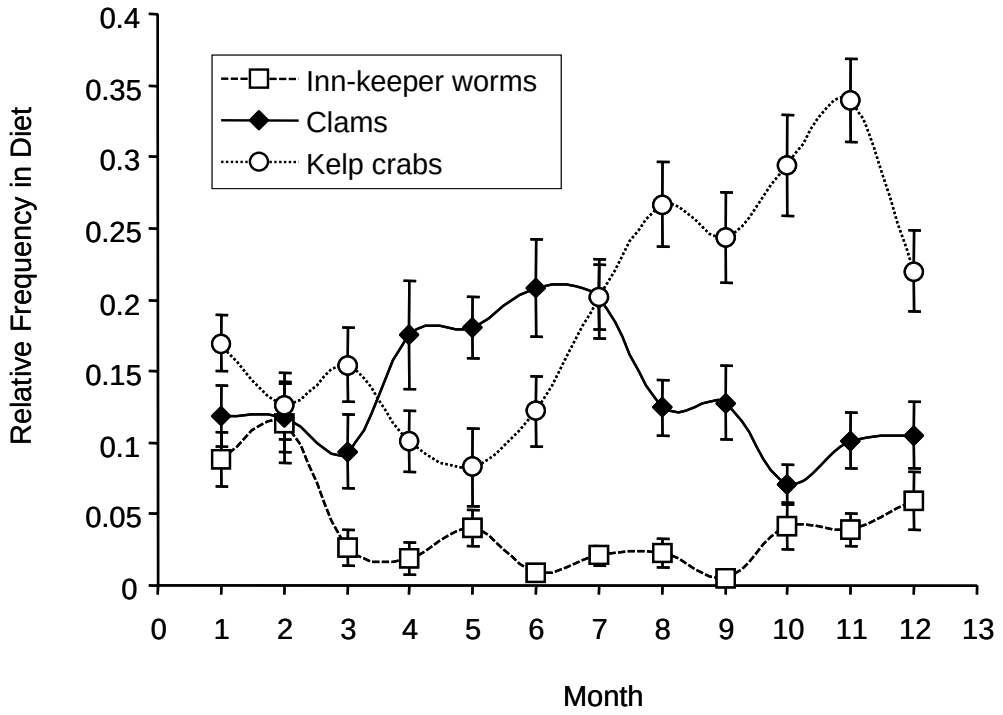

Figure 44. The relative frequency of occurrence (at the population-level) is shown for three prey types over the course of one year, illustrating patterns of seasonal variation observed in sea otter diets.

Individual otters had much more specialized diets, with 80% of the diet of a typical study animal consisting of only 3 prey types. This difference between individual- and population-level diets was reflected in a mean *PSI* score of 0.54 (Table 14).

Table 14. Means and standard errors of the proportional similarity index (*PSI*) are shown for various sub-groups of the population, for all animals in the current study, and for all animals in a similar study conducted in the 1980's (Estes et al. 2003b).

Group	Mean	Std. Error	Result of statistical test
Site 1	0.57	0.025	No significant difference,
Site 2	0.49	0.036	F = 3.93, P = 0.052, power = 0.86
Type 1 diet specialists	0.64	0.029	All pairwise comparisons
Type 2 diet specialists	0.51	0.023	significant,
Type 3 diet specialists	0.29	0.054	F = 17.57, P < 0.0001
All animals, current study	0.54	0.021	Significant difference,
1980's study	0.68	0.032	t = 2.47, P = 0.016

The *PSI* score at site 2 (0.49) was slightly lower than site 1 (0.57), although this difference was not statistically significant (Table 14). The low *PSI* scores indicate a high degree of variation in diet between individuals; however, cluster analysis suggested that individuals

could be classified into three distinct groups based on the prevalence of prey types (Figure 45). Individual otters were easily partitioned into the three diet groupings by discriminant analysis (Figure 46), and jack-knife re-sampling of the data resulted in correct group assignment 93% of the time (Appendix B). The prey types that contributed most to discrimination of the groupings were *Cancer* crabs, abalone, clams, worms (primarily fat innkeeper worms, *Urechis caupo*), mussels and turban snails. Diet type 1 was characterized by large prey such as crab and abalone, type 2 was comprised of small to intermediate size prey (particularly clams, mussels and worms) and type 3 consisted almost entirely of snails (Figure 47). The *PSI* scores differed between diet types (Table 14), with type 1 specialists having the highest overlap with the population diet and type 3 showing the greatest degree of specialization. The most frequently observed specialization was type 2 (57% of study animals), followed by type 1 (33%) and then by type 3 (10%). There was little support for differences in the relative frequency of the three diet types between study sites, or between males and females (the log-linear model providing the best fit to the data included neither interaction term, BIC = –15).

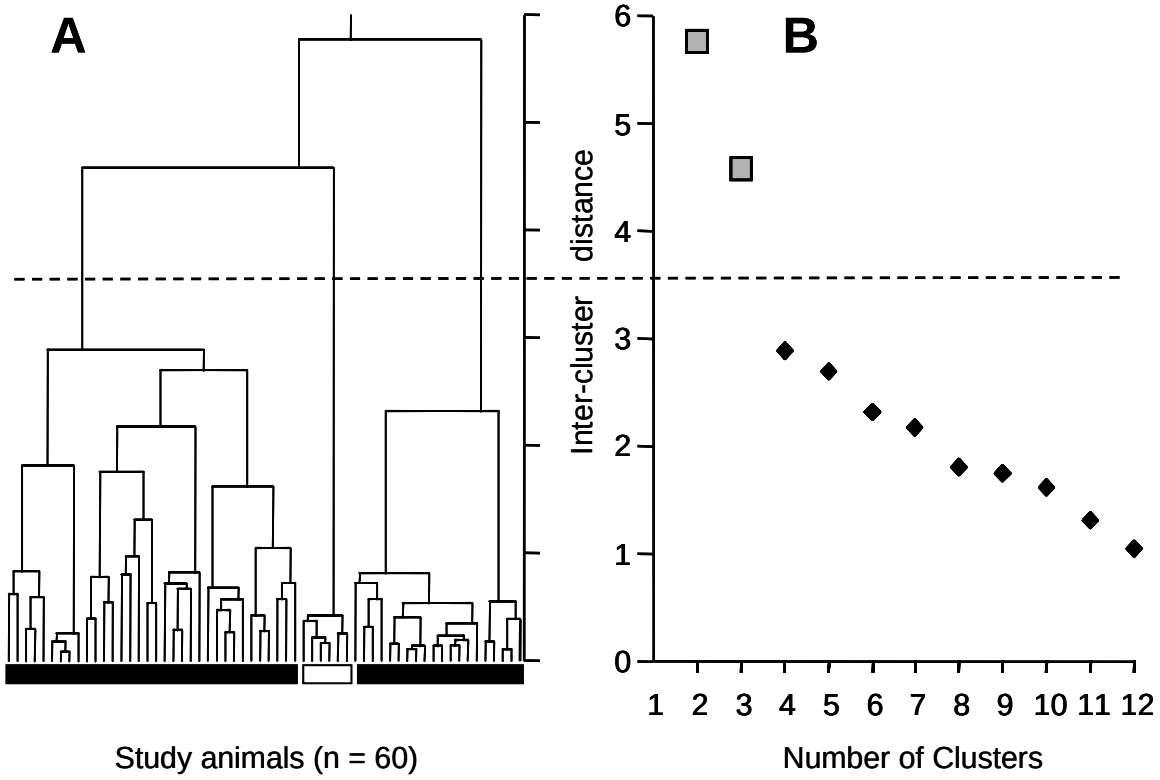

Figure 45. The results of a cluster analysis used to detect natural groupings of diet composition among individual sea otters (sample units) based on their consumption of 13 prey types. A) Dendrogram showing hierarchical relationships between sample units, with branch length indicating the relative distance between adjacent nodes (the terminal nodes represent the individual otters). B) Scree plot of the minimum inter-cluster distances plotted against the number of clusters considered as "real" groupings. The horizontal dashed line shows the cut-off point actually selected, resulting in 3 clusters.

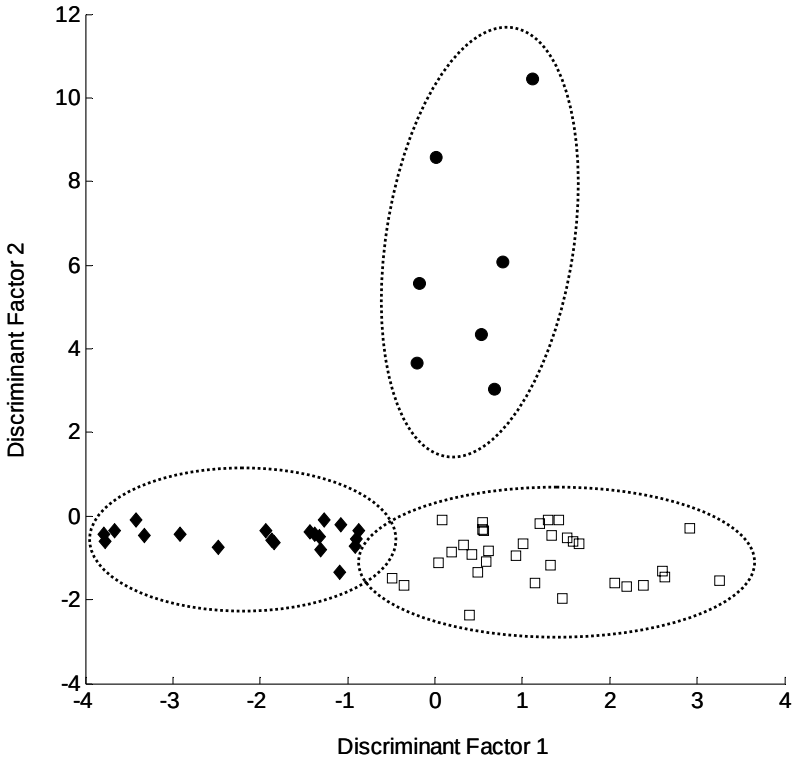

Figure 46. Discriminant Analysis scores are plotted for the two discriminant factors, which represent multivariate ordinations of 13 prey types. Data points represent individual otters, which have been classified by the cluster analysis into one of three groups based on their diet composition (type 1 = filled diamonds, type 2 = open squares, type 3 = filled circles). Diet types are well discriminated into distinct groupings along the two axes.

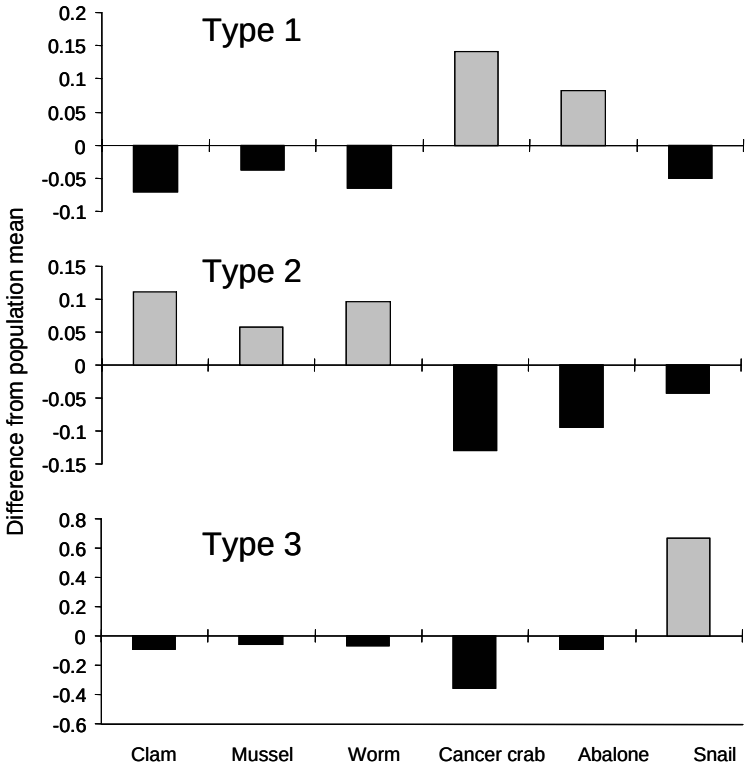

Figure 47. The relative frequency of six prey types are shown for the three types of diet specialist. Relative frequency was calculated as the proportion of the diet comprised by each prey type (in terms of wet edible biomass), and values were standardized by expressing them as differences from the population mean.

Principle Component Analysis indicated that 87% of the individual variation in dive behavior could be explained by 3 factors (Appendix C). The first factor explained 40% of the total variance, and was most closely associated with prey handling time, ST variation and the dive success rate (frequency of successful dives). The second factor explained 26% of the variance, and was most closely related to the number of items captured per dive and SDR. The only variable to load heavily on the third factor was dive duration (Appendix C).

The ordination of individual otters on factors 1 and 2 showed that differences between the three diet types accounted for much of the variation in these two axes of behavior (Figure 48). Individual scores on Factor 1 and 2 differed significantly between diet types (Factor 1 $F=4.35$, $P_{adj}=0.044$; Factor 2 $F=9.25$, $P_{adj}=0.037$), but not between sexes (Factor 1 $F=0.53$, $P_{adj}=0.849$; Factor 2 $F=0.31$, $P_{adj}=0.607$, power = 0.86) or study sites (Factor 1 $F=0.03$, $P_{adj}=0.994$; Factor 2 $F=1.64$, $P_{adj}=0.508$, power = 0.86). We were unable to detect significant differences in Factor 3 between diet types ($F=0.306$, $P_{adj}=0.965$, power = 0.77), sexes ($F=0.756$, $P_{adj}=0.708$, power = 0.86) or study sites ($F=3.284$, $P_{adj}=0.179$, power = 0.86). Foraging behavior varied considerably between foraging bouts, even those recorded for a single study animal: within-animal variation in foraging behavior accounted for 49% of the combined variance of the three principal components. Of the remaining variance, a higher proportion (29%) was explained by differences between specialist types than was explained by individual variation within specialist types (22%).

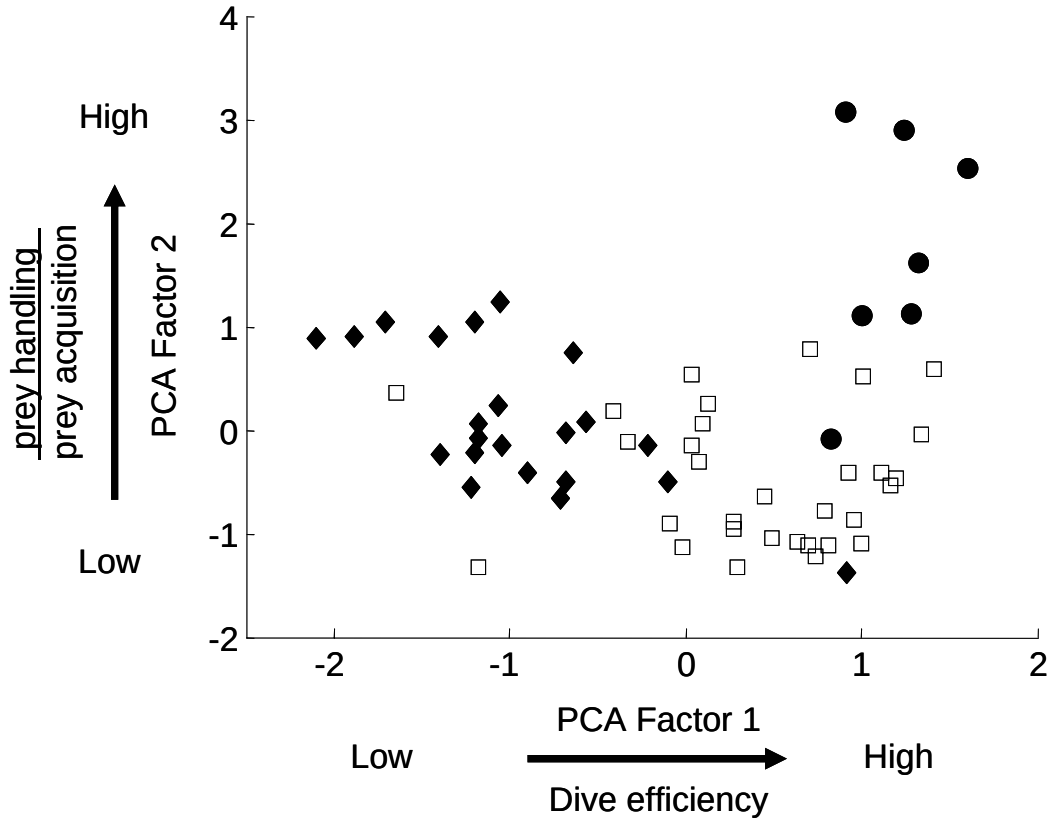

Figure 48. Factor scores are plotted for the first two ordination axes from a principal component analysis of foraging behavior. Data points represent individual otters, classified by diet composition (type 1 = filled diamonds, type 2 = open squares, type 3 = filled circles). Factor 1 represents an axis of dive efficiency: at one end are animals with low dive success rates, variable dive durations and large/rare prey with long handling times, while at the other end are animals with high dive success rates, consistent dive durations and small/abundant prey with fast handling times. Factor 2 represents the ratio of prey handling effort to prey acquisition effort: animals with high values along this axis captured many prey items per dive and had long surface intervals following successful dives, while animals with low values along this axis captured few items per dive and had shorter surface intervals following successful dives, allocating more time (and thus effort) to prey acquisition at the bottom.

The estimated mean rate of energy gain while foraging for all animals in the current study was 29.4 $kJ \cdot min^{-1}$, but this rate varied between individuals and also showed considerable variation from bout-to-bout (within-individual variance; Table 15). The mean rate of energy gain was slightly higher for animals at site 2 ($F = 4.15$, $P = 0.049$), and there were differences between the three diet specializations ($F = 12.63$, $P < 0.001$). Type 1 specialists had a higher rate of energy gain than type 2 and type 3 specialists (Table 15), but also tended to have higher within-individual variance (the difference was significant for females with large pups, $F = 5.70$, $P = 0.013$, but not for females without pups, $F = 2.32$, $P = 0.113$, power = 0.48). The reproductive status of females did not affect the mean rate of energy gain ($Z = -0.67$, $P = 0.501$, power = 0.43) but did affect the variance: females with large pups experienced less bout-to-bout variation in foraging success ($Z = -3.21$, $P = 0.001$). Within-individual variance in foraging success could have important consequences for individual fitness: for example, despite the substantial differences between specialist types in the mean

rate of energy gain, type 2 specialists had about the same probability of exceeding a critical rate of energy gain (on any given bout) as type 1 individuals (Figure 49).

The estimated rate of energy gain while foraging was a good predictor of female body condition (Figure 50), a result consistent with the hypothesized relationship between foraging success and individual fitness. Based on the estimated energy requirements for maintenance metabolism, we estimated that female study animals (without pups) would need to spend 42.3% (±15.78) of their time foraging. This estimated foraging effort closely matched the time-activity budgets collected from study animals, which indicated that females spent an average of 41.9 % (±15.43) of their time foraging (Figure 51).

The fitness surface created by plotting the net rate of energy gain (w_i) as a function of foraging behavior took the shape of a saddle, with two peaks separated by a deep trough: the highest peak corresponded to type 1 specialization, while the second, slightly lower peak corresponded to type 3 specialization (Figure 52). A general linear model fit to the data showed that the first two principal components of behavior accounted for a significant amount of variation in the net rate of energy gain ($R^2 = 0.374$, $P = 0.001$). There was a significant interaction between these two primary axes of behavior ($P = 0.038$), indicating a substantial correlational selection gradient ($\gamma = 0.593$).

Table 15. Means and standard deviations in the estimated rate of energy acquisition while foraging ($kJ \cdot min^{-1}$) by sea otters. Two components of variation are shown, the within-individual variance (between-bout variation) and the between-individual variance. Data for all study animals are summarized for each study site and for both sites combined. Data for adult females without pups and for adult females with large pups are also summarized for both study sites combined, and for each of the three types of diet specialization (see text for details).

					Prey specialization		
Demographic Group	Parameter	Site 1	Site 2	Both Sites	Type 1	Type 2	Type 3
All study animals	**Mean**	**25.6**	**37.2**	**29.4**			
	within-individual σ	16.98	30.16	20.58			
	between-individual σ	11.71	17.65	14.56			
Females without pups	**Mean**			**31.1**	**38.8**	**20.5**	**25.2**
	within-individual σ			19.33	30.26	10.38	12.72
	between-individual σ			15.43	17.99	7.70	4.23
Females with large pups	**Mean**			**43.5**	**45.3**	**19.4**	**44.4**
	within-individual σ			9.98	26.66	1.64	4.50
	between-individual σ			44.9	37.54	12.90	50.63

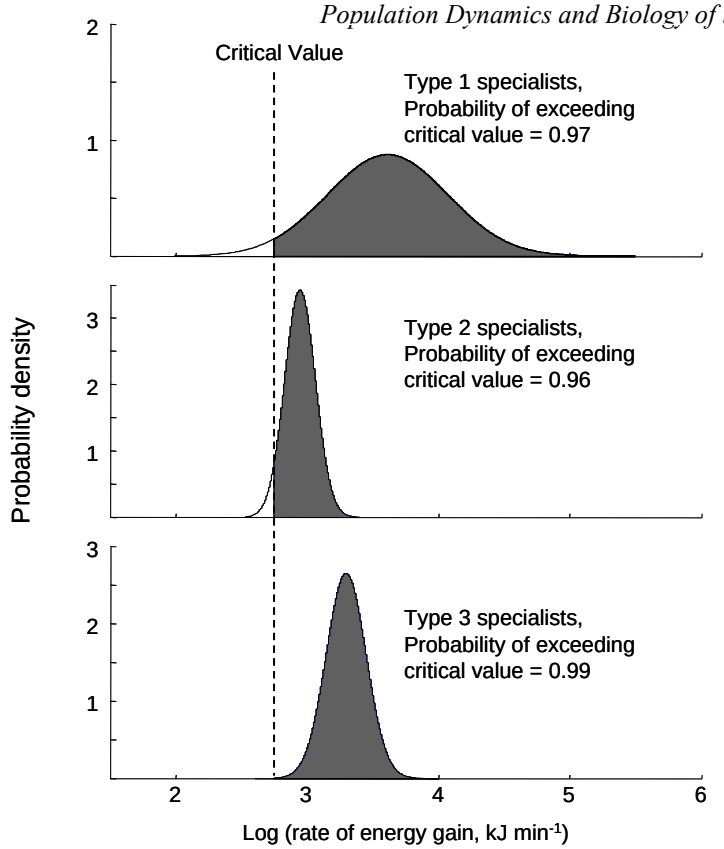

Figure 49. Probability density functions of the rate of energy gain for female otters (with large pups), plotted separately for individuals of each prey specialization type. The vertical dashed line represents an arbitrary "critical value", calculated as 90% of the average rate that would be required for an 18 kg female foraging for 65% of the day (based on published estimates of sea otter metabolic requirements). Note that rates of energy gain were log-transformed because the rate of energy gain was found to be distributed as log-normal.

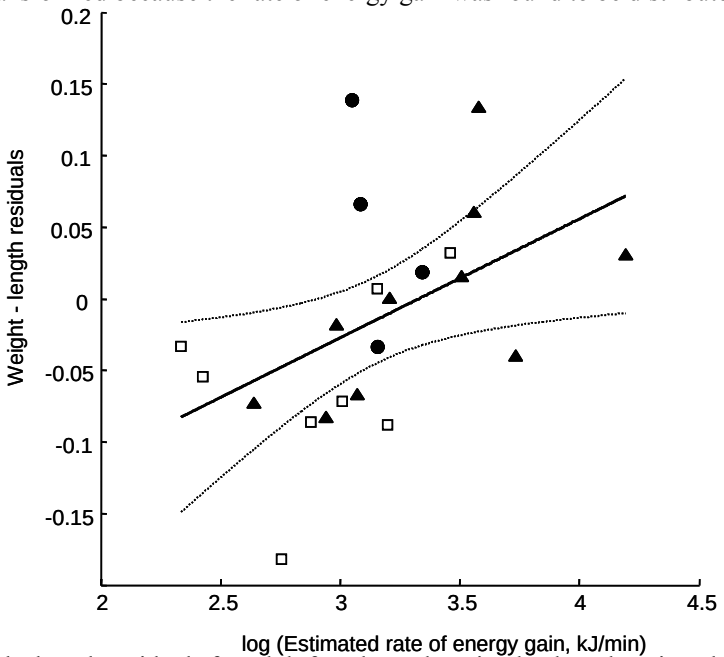

Figure 50. Weight-length residuals for adult female study animals plotted against the estimated rate of energy gain while foraging (log-transformed). Individual otters are classified by their diet specialization: type 1 = filled diamonds, type 2 = open squares, type 3 = filled circles. The solid line shows the least-squares linear regression fit to the data, and dashed lines indicate 95% confidence intervals for the predicted relationship (R^2 = 0.22, P = 0.027), indicating that body condition increases as a function of foraging success.

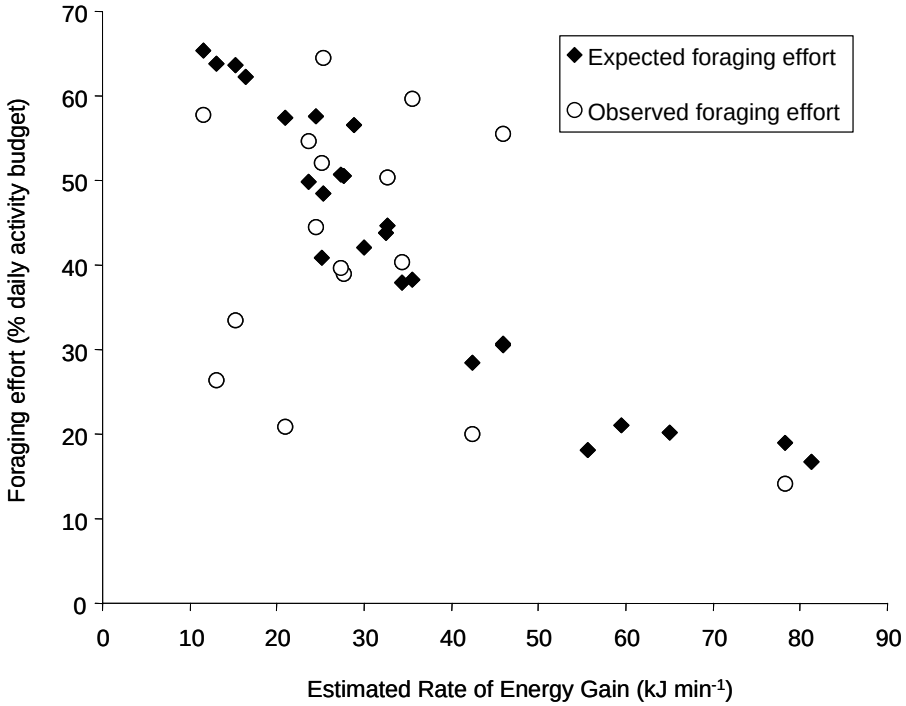

Figure 51. Foraging effort (percent of time spent foraging) plotted against estimated rate of energy gain while foraging. Expected values (filled diamonds) were calculated based on the amount of foraging time that would be needed to meet maintenance requirements, accounting for body weight. Actual percent time foraging was measured for some of the study animals using 24-hour focal animal monitoring sessions: these points (observed foraging effort) are shown as open circles.

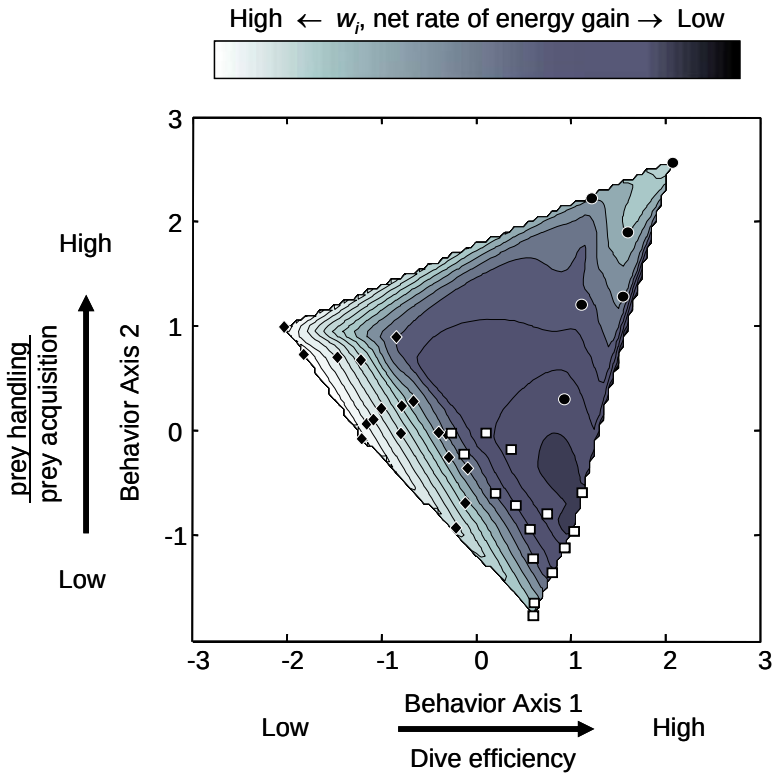

Figure 52. An ordination of the first two principal components of foraging behavior, with a fitness surface superimposed as a contour map: contour elevation corresponds to the net rate of energy gain, wi. The fitness surface was calculated using a multivariate cubic spline algorithm (see text for explanation), and the smoothing factor used (λ= –0.9) resulted in a GCV score of 0.017 and an effective number of parameters of 7.5. Individual otters are also plotted, classified by their diet specialization: type 1 = filled diamonds, type 2 = open squares, type 3 = filled circles.

Discussion

The data reported here demonstrate that southern sea otters have a diverse and variable diet, a finding consistent with previous studies (Ostfeld 1982, Faurot et al. 1986, Kvitek and Oliver 1988, Ralls et al. 1995, Estes et al. 2003b). Six prey categories – kelp crabs, Cancer crabs, urchins, turban snails, clams and mussels – comprised approximately 80% of the diet at both study sites, although the order of importance differed (Table 13). The spatial differences in prey frequency could reflect different abundances of prey species between the sites, but may also reflect sampling error: because of high degree of individual dietary variation, some differences are to be expected simply based on the frequency of specialists of each type included in the sample. Interestingly, this same suite of prey types, with the exception of clams, were predominant in the diet of sea otters studied 20 years ago (Estes et al. 2003b), and 30 years ago (Costa 1978) at Monterey Peninsula. At the level of the population this indicates a fairly consistent diet composition over time, with one notable exception: abalone occurred on a substantially higher proportion of feeding dives in the previous studies (Costa 1978, Estes et al. 2003b). Seasonal trends in diet composition observed in the current study (Figure 44) probably correspond to temporal changes in local abundance for some prey types such as crabs (Carroll 1982), while for other species the relative importance in the diet may increase as a function of seasonal changes in energetic

content, associated with reproduction and gonad development (J. Pearse, *pers. comm.*). A similar phenomenon has been reported for Alaskan sea otters, with respect to seasonal variation in urchin consumption (Watt et al. 2000), and is likely to occur for a variety of prey species.

In contrast to the diverse population diet, individuals tended to specialize on a much smaller suite of prey species. Only 3 prey types comprised 80% or more of the diet for a typical individual, reflecting a mean niche overlap of only 50% between individuals and the population as a whole (Table 14). This represents a relatively high degree of individual specialization (Bolnick et al. 2003), well within the range reported for other highly specialized foragers such as Cocos Island finches (Werner and Sherry 1987) and snails of the genus *Nucella* (West 1986, 1988). Although previous research has clearly shown that individual variation in diet is typical of this sea otter population (Ostfeld 1982, Lyons 1991, Estes et al. 2003b), it appears that the degree of specialization has actually increased since the 1980s (Table 14). Individual specialization is expected to become more pronounced as the degree of intraspecific competition intensifies (Glasser 1982), and the increased specialization seen here may be associated with less abundant food resources (Schindler et al. 1997).

Dietary variation among individuals was not random, but was clearly grouped into three distinct diet specialization types (Figure 45 and Figure 46). It should be emphasized that the dietary characterizations of each diet type (Figure 47) are based on relative importance only, and do not indicate inflexible rules of prey selection. Almost all of the study animals were observed to capture at least 10 different prey types over the three year study period; however, only a few species comprised the bulk of the diet for each individual. Two prey species that were relatively common among all diet types were kelp crabs and urchins: because of their ubiquity, these prey types contributed very little to the discriminant analysis (Appendix B). However, although kelp crabs and urchins occurred on a relatively high percentage of recorded foraging dives (Table 13), their contribution to the population diet on a per-mass basis was much less, due to the small size of each prey item (Ebert 1968, Costa 1978, Mathews 1996). It is also important to note that the relative frequencies of prey species within each diet type varied somewhat from animal to animal: for example, some type 2 specialists preyed mostly on mussels and urchins, while others consumed mostly clams, worms and other sand-bottom infauna (e.g. sand dollars, mole crabs). Indeed, the cluster analysis dendrogram suggests that further divisions of the main groupings could certainly be made (Figure 45); however, based on the distribution of inter-cluster distances and on the unequivocal results of the discriminant analysis (Figure 46), we believe the three groups we have identified provide the most generalized and robust approximation to the data.

Variation in the foraging behavior of sea otters, as described by a variety of measurable characteristics of feeding dives, was well explained by three orthogonal axes: these axes could be conceptualized as dive efficiency, effort allocation (the ratio of prey handling effort to prey acquisition effort) and total dive duration (the latter is actually a proxy measurement for dive depth, because these two variables are closely linked; USGS, unpublished data). Although these axes were derived independently of prey species identity, they nonetheless were closely related to diet composition, such that the three dietary specializations could be

described by their location along the first two behavioral axes (Figure 48). Type 1 specialists, which preyed on large, energy-rich prey types such as *Cancer* crabs and abalone, were characterized by low dive efficiency (low success rate, few prey items per successful dive, long handling time per prey item, and highly variable dive and surface intervals) and a low to intermediate ratio of handling effort to acquisition effort. Type 2 specialists, which preyed on small or intermediate-sized prey such as clams, mussels and inn-keeper worms, were characterized by high dive efficiency but a low ratio of handling effort to acquisition effort (i.e. more time was devoted to acquiring prey from the bottom than to handling at surface). Type 3 specialists, which preyed almost entirely on turban snails, were characterized by very high dive efficiency and a high ratio of handling effort to acquisition effort. Clear differences in feeding behavior (along the first two axes) were found between the three diet types, suggesting that each combination of diet and feeding behavior represents a distinct foraging strategy. Although considerable variation in foraging behavior was attributable to within-individual variation (almost half of the observed variance), approximately two thirds of the between-individual variation was explained by differences between specialist types.

The relatively even distribution of foraging strategies across study sites and among males and females was interesting, and suggests that mechanisms responsible for maintaining alternate strategies within the population are consistent across space, and apply equally to males and females. Because all study animals included in this analysis were adults, it is impossible to determine at this point whether there is any relationship between age-class and foraging strategy: however, based on anecdotal observations of tagged juvenile otters that were not included in this analysis, it appears likely that all three strategies occur among immature animals as well as adults.

The estimated rate of energy gain during foraging bouts varied greatly, both between and within individuals (Table 15). Averaging across all study animals, the prey consumption rate was lower than values previously reported for this population (Costa 1978, Mathews 1996, Jolly 1997), and also low compared to values reported for sea otter populations in Alaska (Garshelis et al. 1986, Doroff and Degange 1994, Dean et al. 2002). The only comparably low prey consumption rate reported in the literature was measured at Green Island in Prince William Sound, Alaska, in a population that was considered to be food-limited at the time of study (Garshelis et al. 1986). It is likely that differences in the reported rates of energy acquisition to some extent reflect the different methodologies used to collect observational data and estimate foraging success. An important potential source of error is the database of energy content values used in the computation of the estimate, which in our analysis was derived from the published literature (Appendix A). Ideally the energy content values would be measured from prey items of each species and size class collected from the actual study sites, to properly account for spatial and seasonal variation. Nonetheless, given the concordance between the predicted foraging effort and the observed activity budgets (Figure 51) it is reasonable to conclude that the rates of energy gain estimated here were not overly biased, and truly reflect a relatively low rate of foraging success. The fact that foraging success is important to individual fitness is demonstrated by the relationship between rate of energy gain and female body condition (Figure 50). The weight/length residuals were, without exception, negative for females whose rate of energy gain was below

20 $kJ \cdot min^{-1}$: interestingly, this value closely matches the predicted maintenance requirement of 19.6 $kJ \cdot min^{-1}$ for an 18 kg female (the average weight of females in this study) that foraged for 65% of the time (the maximum foraging effort recorded during 24-hour focal-animal sessions).

A great deal of the individual variation in the rate of energy acquisition was explained by differences in foraging strategy (Table 15). Type 1 specialists had the highest mean foraging success rate overall, but variation between individuals was much higher than the other two strategies, as was within-individual (between-bout) variance. Specializing on crabs, abalone and other large prey types clearly has the highest potential pay-off in this population, but it is also a much riskier strategy than specializing on smaller, more abundant prey. When the relationship between fitness and forage success is non-linear, as is the case for many species, it is necessary to consider the variance as well as the mean rate of energy gain because, under certain circumstances, individuals are expected to choose a less risky strategy (lower variance) over one with a higher mean pay-off (Real and Caraco 1986, McNamara and Houston 1992, Kacelnik and Bateson 1996). High-variance strategies are likely to be avoided when an individual's expected success rate exceeds some critical value (i.e. the value needed to reproduce or survive), and failure to exceed the critical value is associated with costs outweighing the potential benefits of achieving a higher mean (Caraco and Gillespie 1986, Gillespie and Caraco 1987, Barkan 1990). For female sea otters, successfully rearing a pup requires a substantial investment of resources, and during lactation females likely exhaust whatever reserves they have stored prior to parturition (Monson et al. 2000). Failure to regularly meet the basic energy requirements for maintenance at this stage is likely to result in the loss of the pup or, at the extreme, female mortality. Foraging success will thus be under particularly intense selection during the latter stages of lactation, and there may be a selective trade-off between maximizing the mean rate of energy return and minimizing the variance. Probability density functions corresponding to the observed mean and variance in foraging success for each strategy show that, despite the higher mean success rate of type 1 specialists, the likelihood of failing to meet a critical rate of energy gain on any given foraging bout is almost identical for type 1 and type 2 specialists (Figure 49). This trade-off between mean and variance in the rate of energy gain may to some extent balance the relative benefits of the different strategies.

The adaptive landscape formed by plotting rate of energy gain against foraging behavior illustrates another reason that distinct foraging strategies can coexist within this population: there are at least two local fitness maxima (i.e. local peaks in foraging success; Figure 52). Type 1 specialists occupy the higher peak, while type 3 specialists are centered on a slightly lower peak. The low rate of energy gain achieved by individuals that exhibited more "generalist" behavior (i.e. their position on the ordination placed them between the modes associated with the three diet types) results in a deep trough between the two peaks. A strong interaction between the principal axes of behavior means that these traits jointly determine foraging success: a combination of large prey size, low dive efficiency and intermediate ratio of handling/acquisition effort results in high forage success, as does a combination of very small prey, high dive efficiency and high ratio of handling/acquisition effort, but all other combinations result in low success.

Type-2 specialization would appear to be sub-optimal, based on their position on the fitness surface: type 2 specialists are clustered along the "slope" leading up to the higher fitness peak (Figure 52). This may or may not be the case: factors not included in the model (e.g. shorter travel time to foraging patches, etc.) could actually increase the realized fitness for type 2 specialists, as could a trade-off between the mean and variance in the rate of energy gain (see above). Moreover, the strong correlational selection gradient suggests that frequency dependence is likely responsible for maintaining multiple fitness peaks (Sinervo and Svensson 2002). Frequency-dependent selection is inherently dynamic, with alternative foraging strategies in a cyclic "game" based on prey abundance (e.g. Ehlinger 1990, Beauchamp et al. 1997), and so at any given instant there is likely to be a "best" and "worst" strategy (but the locations of these optima will shift over time). If this is the case, what prevents type 2 specialists from simply switching to a more profitable strategy? Individual sea otters probably cannot easily switch to a different foraging strategy because of the difficulty of learning the skills required to efficiently capture and handle the new prey types (Werner et al. 1981, Estes et al. 2003b). The time required to master new foraging skills would determine the magnitude of the cost (in terms of decreased energy gain) associated with a switch from one foraging strategy to another (see Chapter 3 of this dissertation, and Hughes 1979), and the cost of switching may be sufficient to "trap" individuals in sub-optimal strategies. As a result of the lag created by this learning inertia, frequency dependent dynamics are likely quite slow for sea otters, perhaps spanning generations and probably mediated by cultural transmission (Estes et al. 2003b).

Considered together, a number of lines of evidence – the increasing degree of individual specialization, the high percent of the activity budget devoted to foraging, and the generally low prey consumption rates – suggest that this population is becoming increasingly food-limited. However, the considerable individual variation in diet and foraging success means that food-limitation does not act equally on all animals, and this has contributed to our difficulty in diagnosing the status of this population. Moreover, it is very likely that food-limitation is interacting synergistically with other factors that negatively impact population growth, including abnormally high levels of infectious disease (Miller et al. 2002, Kreuder et al. 2003), elevated contaminant burdens (Bacon et al. 1999) and even fisheries-related mortality (otters may be increasingly utilizing greater feeding depths and "sub-optimal" habitats that increase their exposure to fishing activity). More work will be required to fully untangle the role of food limitation in the (apparently) stalled recovery of the southern sea otter.

Chapter 6. Dive Behavior and Activity Budgets

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Abstract

1. We studied the diving behavior and daily foraging effort (measured as percent time spent foraging) in southern sea otters at two locations, San Simeon and Pt. Conception. To accomplish this we combined information collected using radio-telemetry and archival time-depth recorders, or TDR's.
2. We distinguished foraging dives from non-foraging dives using an existing model, which utilizes logistic regression analysis of dive parameters. We then analyzed feeding dive depth, duration and post-dive interval for each of 24 study animals
3. Males tended to utilize greater maximum depths than females: critical foraging habitat for females (the depth range that included 95% of recorded foraging dives) was 2–20m, while for males it was 2–35m. For males, both dive depths and the duration of the post-dive interval were greater at Pt. Conception than at San Simeon.
4. There were significant differences in dive behavior between females that specialized on different prey types, and diet specialization type could be distinguished on the basis of post-dive interval alone.
5. Estimated population-level activity budgets for males and females were almost identical when calculated from 24-hour activity sessions (using radio telemetry and direct observations) or from TDR data, but the latter allow for more in-depth analysis of foraging effort due to the vastly increased sample size.
6. For all 5 males that traveled between the two study sites, less time was spent foraging at Pt. Conception than at San Simeon, and for both males and females the percent time foraging was greater in the current study than in a similar study conducted in the 1980s.
7. The high level of individual variation in dive behavior and foraging effort (25 to 50% time spent foraging for males and females) means that a considerable sample size is required to make population-level inferences based on activity budgets.

Introduction

All marine vertebrate species that exploit sub-surface prey must regularly return to the surface to breathe; thus, their foraging efficiency is ultimately constrained by the amount of oxygen they can store in their tissues, and by their metabolic rate while diving (Boyd et al. 1997, Kooyman and Ponganis 1997). Operating within these common constraints, diving bird and mammal species exhibit a variety of physiological and behavioral strategies, all of which appear to maximize the net rate of energy acquisition subject to differences in life history trade-offs, and prey distribution and density (Kooyman 1989, Costa 1991, Boyd 1998, Tremblay and Cherel 2000, Costa and Gales 2003, Shaffer et al. 2003). As with many terrestrial predators, flexible foraging strategies allow diving birds and mammals to respond to changes in food availability through a variety of behavioral and physiological mechanisms; these include increasing the time devoted to feeding (Costa et al. 1989, Monaghan et al. 1994), changing or expanding diet (Thompson et al. 1997, Croxall et al. 1999, Dellinger and Trillmich 1999, Jaquet et al. 2000), altering dive duration (Culik and Luna-Jorquera 1997) and altering dive depths and/or dive swimming speeds (Boyd et al. 1997, Tremblay and Cherel 2000).

Sea otters are one of the smallest marine mammals, and the only marine mammal to rely exclusively on fur for insulation (Williams et al. 1992). As a result of their small size and lack of blubber, sea otters have extremely high mass-specific metabolic demands (Chapter 7 and 8, this report, Costa and Kooyman 1984) resulting in a limited capacity to store energy, and are therefore highly susceptible to changes in prey availability or other environmental perturbations (Costa 1982, Green and Brueggeman 1991, Brody et al. 1996, Watt et al. 2000, Dean et al. 2002). There is evidence that sea otters can adjust their foraging strategies to changing food availability: previous studies have found that changes in prey abundance may be accompanied by changes in diet (Estes et al. 1981, Ostfeld 1982, Garshelis et al. 1986, Estes 1990, Green and Brueggeman 1991, Watt et al. 2000), changes in dive depth and duration (Kvitek et al. 1993) and, perhaps most importantly, changes in the proportion of activity budget devoted to feeding (Estes et al. 1986, Garshelis et al. 1986, Ralls and Siniff 1990). Additionally, our current research (Chapter 5, this report) suggests that reductions in prey availability may also be associated with an increase in the degree of individual dietary specialization (Estes et al. 2003b). Specifically, we have found that southern sea otters in the center of the range (where densities are high and food may be limiting) tend to fall into one of 3 distinct diet specialization types: type 1 is characterized by large prey items such as crabs or abalone, type 2 is characterized by small to moderate prey items (e.g. clams, worms, mussels), while type 3 specialists feed almost exclusively on turban snails. In view of the predictable differences in diving behavior observed for pinniped species with particular prey specializations (e.g. Costa and Gales 2003), it seems conceivable that these three intra-specific dietary specializations may be characterized by differences in diving behavior.

The ability to accurately measure diving behavior is a key requirement for detecting behavioral and physiological responses to prey availability in diving birds and mammals. The most common tool for measuring diving behavior is the time-depth recorder, or TDR (Kooyman and Ponganis 1997). A small, implantable TDR has recently been developed for use in sea otters (Bodkin et al. 2004), providing a novel means of quantifying foraging behavior and activity budget for this species. Data collected from TDR-implanted sea otters

in Alaska have allowed for identification of key foraging habitat and recognition of multiple diving strategies (Bodkin et al. 2004). Here, we summarize data on dive behavior and time-activity budgets collected by deploying TDR's on southern sea otters in the south half of their range in California. We compare the estimates of percent time foraging with those collected concurrently using a telemetry-based technique (Loughlin 1980, Ralls and Siniff 1990), and discuss the patterns and implications of variation in diving behavior and activity budgets in the southern sea otter.

Methods

Techniques and study design for the capture, instrumentation and re-capture of sea otters are described elsewhere in this report (refer to Chapters 1, 2 and 9 for details). In total we deployed 45 TDR implants (Wildlife Computers, Redmond WA) between spring 2001 and fall 2002: 30 in the northern study area (San Simeon) and 15 in the southern study area (Pt. Conception). The TDR's at Pt. Conception were all deployed into male animals, while the 30 deployments at San Simeon included both females (n=20) and males (n=10). Each TDR was programmed to record depth at 4s intervals (0.25m data resolution) and internal body temperature at 60s intervals (0.1° C data resolution), over a total recording period of 1 year. The model of TDR's deployed in 2001 (Mk7) were limited to 2MB of data storage and thus a duty cycling program of "5-days-on/9-days-off" was used to extend the recording period to span 363 days. The model of TDR's deployed in 2002 (Mk9) had sufficient memory capacity (16MB) to allow for 367 days of continuous recording. Due to a technical flaw, almost all of the instruments failed prematurely (but not catastrophically) resulting in truncated data sets of between 3 months and 1 year in duration.

Retrieval of the TDR's depended on successful recapture of the study animals, a task that proved especially challenging at Pt. Conception due to difficult field logistics combined with elusive animal behavior. At present time we have retrieved 27 of the 45 deployed TDR's, 24 of which were from San Simeon study animals and only 3 of which were from the Pt. Conception deployments. Fortunately, 3 of the male study animals from the northern study area made seasonal movements to Pt. Conception, thus providing us with additional dive data from Pt. Conception and increasing the sample size for that area to 6. Of the 27 recovered TDR's, 3 had corrupted data files and at the present time are un-usable, thus we restrict our analyses to the remaining 24 TDR records.

Having recovered raw data from the TDR's, initial processing was conducted using IKNOS toolbox (developed using the MATLAB technical computing language by Y. Tremblay, unpublished). The IKNOS dive analysis module was used to correct for drift in the depth considered to represent the surface (referred to as "zero-offset" drift of the instruments), and identify the beginning and end of the dives. Dives were considered as immersions to a minimum of 2 meters (4 times depth resolution of the instruments), for at least 12 seconds (3 times sampling interval). Standard parameters were calculated for each dive (Figure 53), including the maximum dive depth, duration of the sub-surface interval (DT), duration of time at spent at the bottom of the dive (BT) but not necessarily on the ocean floor, duration of the post-dive surface interval (or PDI, the time elapsed until the next dive), descent rate (vertical swim-speed from surface to bottom) and ascent rate (vertical swim-speed from

bottom to surface). Time spent at the bottom for each dive was calculated as the interval between the moment the animal reduced its mean descent speed by ≥70%, and the moment the animal started ascending at ≥ 30% of mean ascent speed (Tremblay, unpublished).

After initial processing, our first step was to distinguish foraging dives from non-foraging dives. Because sea otters are benthic foragers and then conduct all prey handling at the surface, their feeding dives can be distinguished from non-feeding dives based on measurable characteristics of the time-depth profile. Making use of this fact, Bodkin *et al*. (2004) have developed a method for categorizing dives into feeding and non-feeding dives using the logistic regression equation:

$$\log\left(\frac{P}{1-P}\right) = \alpha + \beta_1 * k_1 + \beta_2 * k_2 \mathrm{K} + \beta_i * k_i \qquad 42$$

where α is a constant and β_t are the slope parameters associated with the independent variables k_i. The independent variables we utilized were dive duration, the ratio of bottom time to dive duration (BT/DT), ascent rate, descent rate, and two interaction terms: dive duration×ascent rate and BT/DT×descent rate. We applied equation 42 to our data set (model parameterization was identical to Bodkin et al. 2004), and classified all dives with P>0.5 classified as feeding dives.

Detailed analyses of feeding dives were conducted for each individual study animal, and four descriptive statistics (mean, standard deviation, median and modal value) were calculated for three key dive parameters: dive depth, dive duration and post-dive interval. These data are summarized for all animals in Table 16. In the case of 6 males that periodically moved between study areas, separate analyses were conducted for periods at Pt. Conception vs. San Simeon. We also conducted separate analyses for females during periods when they were without pup and during periods when they had dependant pups, and for all animals we analyzed day-time and night-time dives separately (day vs. night designation for each dive was assigned based on the local sunrise and sunset times). We tested each dive parameter for effects of sex, study area (in the case of males), female reproductive status, and day vs. nighttime foraging.

Table 16. Foraging dive statistics are shown for 24 sea otters, grouped by sex, location and diet type. Group means are also shown (±95% confidence intervals).

		# dives	Dive Depth				Dive Duration				Post-Dive Interval			
Otter ID	Diet Type	recorded	Mean	Std. Dev.	Median	Mode	Mean	Std. Dev.	Median	Mode	Mean	Std. Dev.	Median	Mode
Females, San Simeon														
6 - 41	1	8502	12.48	4.216	13.0	12	99.09	26.920	100	98	58.75	68.225	36.0	29
6 - 458	1	19807	16.23	5.864	16.5	17	110.87	34.146	112	111	63.45	65.052	44.0	30
7 - 595	1	49686	4.82	1.863	5.0	5	60.33	29.763	56	28	38.36	48.490	24.0	21
6 - 622	1	21024	9.26	2.486	9.5	10	95.33	29.349	100	107	58.48	59.691	40.0	28
7 - 629	1	62691	5.60	2.934	5.0	5	72.16	21.861	72	68	37.75	58.343	20.0	17
7 - 690	1	77126	10.76	4.256	10.0	9	106.70	34.780	108	108	65.56	73.004	40.0	30
Type 1 mean value:			**9.86**	**(± 3.44)**			**90.75**	**(± 16.09)**			**53.72**	**(± 9.95)**		
6 - 89	2	12686	4.49	2.396	4.0	3	65.66	18.987	64	64	34.11	40.183	24.0	17
6 - 446	2	22692	7.46	2.577	7.5	7	72.65	19.659	72	76	32.49	41.076	24.0	21
6 - 495	2	3783	4.64	1.865	4.5	4	60.26	22.251	60	60	27.60	35.579	20.0	17
6 - 642	2	44277	7.91	2.864	7.5	8	85.26	23.526	84	88	35.10	40.723	24.0	21
Type 2 mean value:			**6.13**	**(± 1.77)**			**70.96**	**(± 10.58)**			**32.32**	**(± 3.26)**		
6 - 769	3	11810	13.02	5.978	11.0	9	108.24	34.602	108	100	97.14	81.436	72.0	44
6 - 781	3	45679	8.86	3.520	8.5	7	85.53	23.958	84	87	74.68	68.007	56.0	32
Type 3 mean value:			**10.93**	**(± 4.08)**			**96.88**	**(± 22.26)**			**85.91**	**(± 22.01)**		
6 - 157	n/a	3484	8.78	3.143	8.5	7	72.37	23.843	72	75	75.58	84.199	44.0	29
6 - 654	n/a	26185	8.24	3.234	7.5	7	83.55	23.204	84	83	49.29	55.384	36.0	28
All females mean value:			**8.75**	**(± 1.81)**	1.811	3.45717	**84.14**	**(± 9.25)**	9.245	17.6485	**53.45**	**(± 10.73)**	10.734	20.4923
Males, San Simeon														
6 - 283	n/a	3187	12.19	8.880	9.0	8	88.67	43.541	76	61	74.76	69.868	56.0	32
6 - 597	n/a	83	5.73	1.558	6.0	6	86.70	29.869	92	102	51.66	56.036	40.0	29
6 - 647	n/a	2994	30.60	6.495	32.5	34	133.96	26.666	132	131	58.04	50.693	52.0	49
7 - 682	n/a	4030	9.87	6.715	8.0	7	108.81	47.469	104	104	29.12	36.990	16.0	8
6 - 183	1	9949	6.23	4.235	5.0	4	72.36	24.809	68	64	49.70	61.706	28.0	22
6 - 544	1	12735	10.14	5.870	9.0	8	90.02	36.360	88	79	44.32	64.057	28.0	19
6 - 259	2	790	12.40	10.044	8.0	5	95.67	45.542	84	71	71.65	72.509	52.0	27
6 - 531	2	14866	19.77	14.139	21.5	5	115.36	50.190	120	142	60.43	56.256	48.0	20
7 - 604	2	7202	8.36	5.873	7.0	6	101.68	37.340	100	100	54.98	69.401	32.0	22
7 - 717	2	52200	8.72	6.412	6.5	6	77.01	45.493	68	30	42.94	53.468	28.0	9
SS males mean value:			**12.40**	**(± 4.66)**			**97.02**	**(± 11.50)**			**53.76**	**(± 8.42)**		
Males, Pt. Conception														
6 - 283	n/a	3527	17.97	8.400	17.5	25	123.68	46.533	124	142	105.70	87.268	80.0	56
6 - 597	n/a	11433	6.70	3.301	6.5	6	78.95	31.098	76	71	55.69	54.103	44.0	28
6 - 647	n/a	9225	31.78	11.292	34.0	34	139.73	40.415	144	145	68.52	57.096	60.0	56
7 - 682	n/a	8647	10.57	6.019	9.0	7	118.77	45.494	112	109	30.74	48.813	16.0	8
6 - 259	2	2442	12.47	7.466	10.0	6	91.55	38.185	84	74	83.46	90.827	56.0	30
7 - 717	2	10950	9.93	5.803	7.5	5	86.94	47.136	88	31	49.06	52.651	36.0	12
PC males mean value:			**14.90**	**(± 7.26)**			**106.60**	**(± 19.32)**			**65.53**	**(± 21.24)**		

At any given instant of TDR deployment, it was possible to classify the behavior of each study animal as follows: if a feeding dive was in progress, or the animal was at the surface but had surfaced from a feeding dive within the previous 10 minutes, the instantaneous behavior was classified as foraging (a 10 minute cut-off was sufficient to encompass the observed surface prey-handling time of 99.9% of >25,000 recorded feeding dives: see Chapter 5); alternatively, if a non-feeding dive was in progress or the animal had surfaced from a non-feeding dive within the previous 5 minutes, the behavior was classified as "active-other"; otherwise, behavior was classified as "inactive". Using these classification criteria, the instantaneous behavior of study animals was determined for every 10 minute interval over the period of deployment, and daily activity budgets were then calculated from the TDR records as the proportion of 10 minute intervals devoted to each behavior over a 24 hour period (Figure 54).

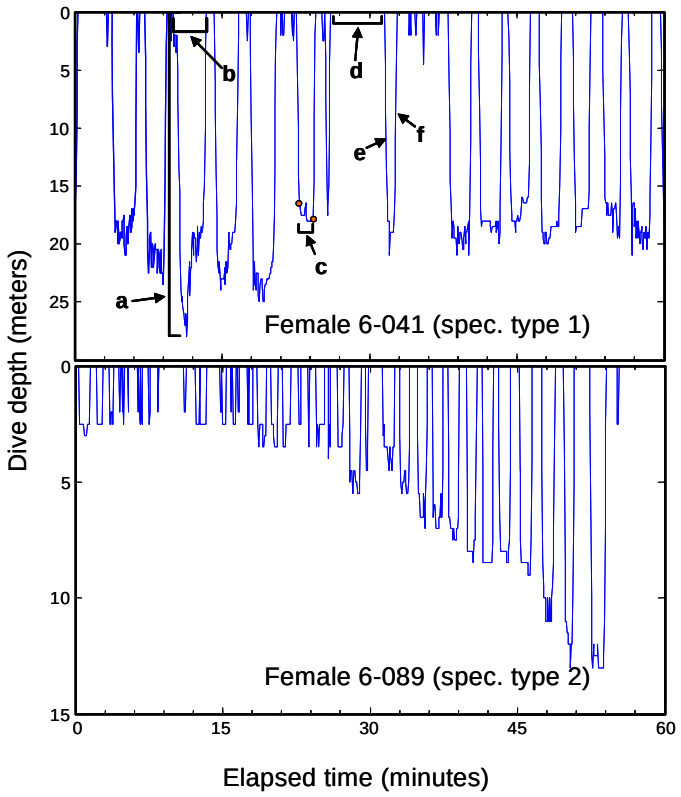

Figure 53. Sample time–depth data profiles over a one hour period for two of the study animals, provided to illustrate typical sea otter feeding dives as measured by time depth recorders (TDR's). The blue lines connect individual depth measurements, with points along the top horizontal axis indicating periods at the surface. Size key statistics that were calculated from the time–depth profiles are shown graphically in the top graph: a) maximum dive depth, b) dive duration, c) time-at-bottom, d) post dive interval, e) descent rate and f) ascent rate. The two profiles shown here illustrate the differences between type 1 diet specialists (female 6-041 at top) and type 2 diet specialists (female 6-089 at bottom), the latter being characterized by shorter/shallower dives and shorter post-dive intervals.

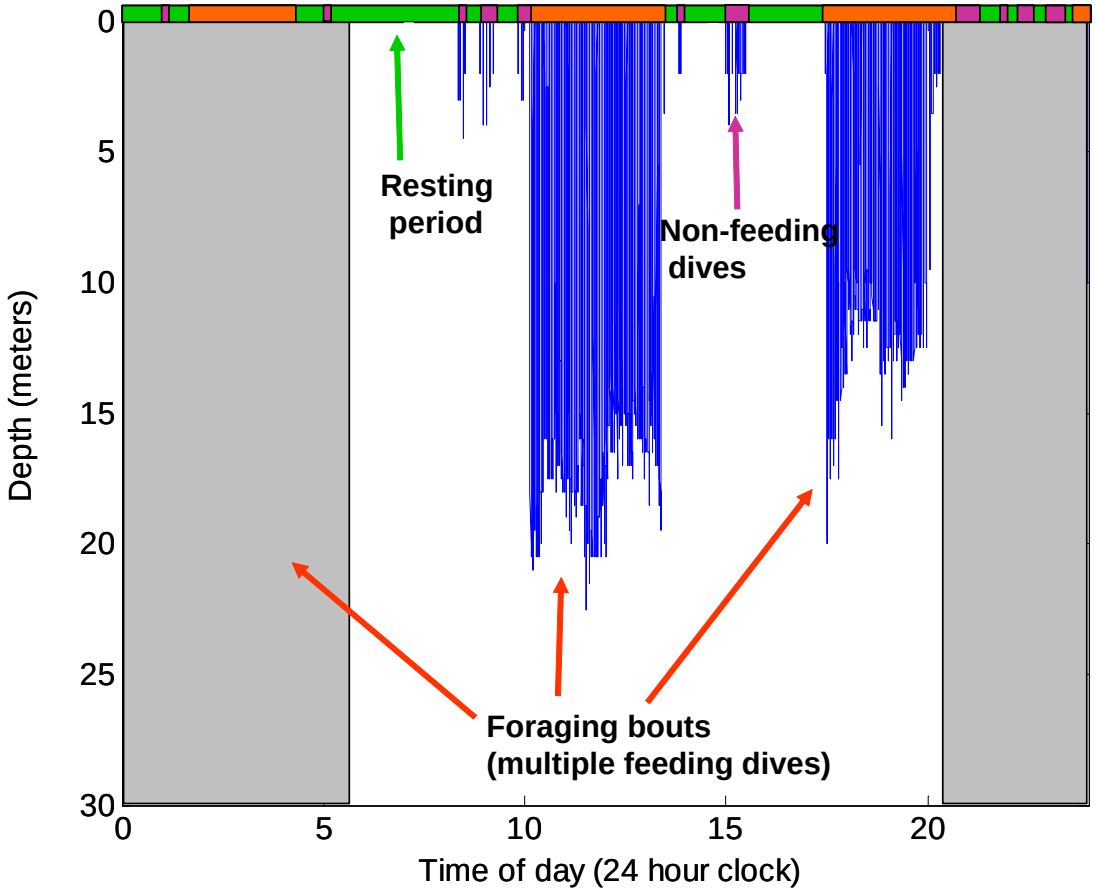

Figure 54. Sample time–depth data profile over a 24-hour period, showing the temporal division of behavior into bouts of forage dives, resting periods and non-feeding dives. The horizontal bar at top indicates the activity budget timeline corresponding to this dive profile: orange stripes indicate periods that would be classified as foraging activity, green stripes indicate periods that would be classified as inactive (or resting), and purple stripes indicate periods that would be classified as non-foraging activity.

We also measured activity budgets from study animals using a combination of direct observation and radio telemetry (the temporal pattern of the VHF signal was used to determine behavior, following the methods of Loughlin 1980, Ralls and Siniff 1990). The instantaneous behavior of a focal animal was recorded at 10 minute intervals over a 24-hour recording session, using classification criteria equivalent to that described above. Daily activity budgets were again calculated as the proportion of 10 minute intervals devoted to each behavior; however, in contrast to the TDR records there were periods of time during the 24-hour focal animal sessions when behavior had to be recorded as "unknown" due to poor transmitter signal quality. These unknown periods were removed prior to analysis, and thus the reported activity budgets actually represent proportions of known activity. Unfortunately this introduces the potential for estimate bias (i.e. if any one behavior was more likely to be classified as unknown): to reduce the potential for bias, we limit our analyses here to activity sessions where ≤10% of the intervals were unknown. This restriction results in a total of 24 sessions available for analysis (Table 17).

Table 17. Results of 24-hour telemetry-based activity sessions conducted between 2001 and 2003 in the San Simeon study area.

				Percent time for each activity		
Otter ID	Date	# hours	Status	Feeding	Resting	Other
Females, no pup						
6-769	4/22/2003	24	adult	46.4	39.9	13.8
7-642	7/2/2003	24	adult	49.0	45.5	5.5
6-008	8/28/2001	24	adult	41.7	47.5	10.8
6-089	6/19/2001	24	adult	45.2	46.0	8.9
6-208	8/8/2001	24	adult	39.0	46.6	14.4
6-398	7/15/2003	24	adult	66.7	29.0	4.4
7-595	11/25/2002	24	adult	34.0	48.9	17.0
7-629	1/14/2003	24	adult	55.6	25.7	18.8
6-781	12/10/2002	24	adult	50.4	31.5	18.2
6-041	7/3/2001	24	adult	25.3	65.8	8.9
6-606	4/30/2002	22	adult	20.7	60.3	19.0
6-067	7/11/2001	24	sub-adult	46.3	44.0	9.7
			mean	**43.3**		
			std. deviation	**12.6**		
Females with pup						
7-555	3/3/2003	24	adult (small pup)	52.9	37.7	9.4
6-041	9/11/2001	24	adult (small pup)	25.0	54.4	20.6
6-672	9/16/2002	24	adult (small pup)	31.9	40.3	27.8
7-705	6/3/2003	24	adult (large pup)	60.6	29.6	9.9
			mean	**42.6**		
			std. deviation	**16.9**		
Males						
7-682	8/12/2003	24	adult	23.3	44.4	32.3
7-717	5/6/2003	24	adult (territorial)	40.1	45.1	14.8
6-544	7/29/2003	24	adult	35.6	24.4	40.0
7-616	5/20/2003	24	adult	33.3	40.3	26.4
6-183	11/20/2001	24	adult (territorial)	36.4	40.9	22.7
6-183	7/18/2001	24	adult	41.9	44.2	14.0
6-259	9/4/2001	24	adult	29.5	62.5	8.0
7-604	6/17/2003	24	adult	43.7	43.0	13.4
			mean	**35.5**		
			std. deviation	**6.8**		

We contrasted the activity budget estimates derived from TDR records with those calculated using radio telemetry, to determine whether the two methods provide directly comparable estimates. There were concurrent TDR records for 11 of the 24-hour telemetry-based activity sessions, and there were 14 additional day-time sessions (12-hours) for which there were concurrent TDR records. We excised just the portion of the TDR records corresponding to these 25 telemetry-based activity sessions, and used these to create matching TDR-based activity budget estimates. We then compared the two paired samples, reasoning that if the two techniques provide consistent estimates there should be no net difference in the estimated percent-time foraging; conversely, a difference one way or the other would indicate a prevailing bias in the TDR estimates. To visualize the full distribution of the estimate bias between these two techniques, we randomly sub-sampled 10-hour periods from each of the original 25 sessions, sampling with replacement to create 10,000 boot-strapped replicates.

Using the TDR-derived activity budgets we tested for seasonal differences in activity budget, and we compared nighttime and daytime activity budgets by calculating the relative proportion of all feeding conducted during the day for each study animal. We contrasted the proportion of time spent feeding at Pt. Conception vs. San Simeon for individual males, and comparisons were also made for females with vs. without pups. Finally, we compare the estimates from the current study with those calculated during the 1980's when the population was increasing in this part of the range (Ralls and Siniff 1990).

To assess the effect of sample size on the TDR-derived estimate, we created 10,000 replicate boot-strap samples from our original sample of 24 TDR records, ranging in sample size from 5 to 50, and measured the resulting variance (measured as CV) and confidence interval width for each sample. The effect of sample size on sample variance and estimate precision was then evaluated graphically. We used standard Analysis of Variance to test for differences between mean values, and for contrasts of non-normal distributions (e.g. comparisons of dive-depth profiles) we used 2-sample Kolmogorov-Smirnov (KS) tests. For all pair-wise comparisons we used a wilcoxin signed-rank test. All statistical tests were considered significant at $\alpha = 0.05$ (experiment-wide type-I error rate).

Results

Diving Behavior

The diving behavior of all study animals tended to be divided into "bouts" of distinct activities: foraging bouts (defined as a succession of temporally contiguous feeding dives) lasting 2-4 hours were generally separated by periods of inactivity (presumably resting) of 1-3 hours, while non-feeding dives (traveling or interacting) occurred in shorter bouts, often immediately before or after a foraging bout (Figure 54). Foraging bouts occurred during both the day and night with approximately equal frequency, as has been previously reported based on telemetry data (Ralls et al. 1995),.

In the case of both male and female sea otters, approximately 50% of all feeding dives occurred between 4m and 12m depth; however, males tended to utilize greater maximum depths than females (Table 16), and dive depth frequency-distributions differed significantly between males and females (KS=0.158, P=0.0001; Figure 55). For female sea otters at San Simeon, critical foraging habitat (defined as the depth range including 95% of recorded foraging dives) was 2–20m. For males, critical foraging habitat was 2–35m at San Simeon and 2-40m at Pt. Conception. Dive depth profiles differed greatly between individuals in the case of both males (Figure 56) and females (Figure 57). Some study animals of both sexes utilized a very narrow range of depths, resulting in a sharply-peaked, unimodal depth frequency distribution. In contrast, other individuals were characterized by a fairly even utilization of a broad range of feeding depths, while still others (particularly males) exhibited a distinctly bimodal depth frequency distribution (Figure 58).

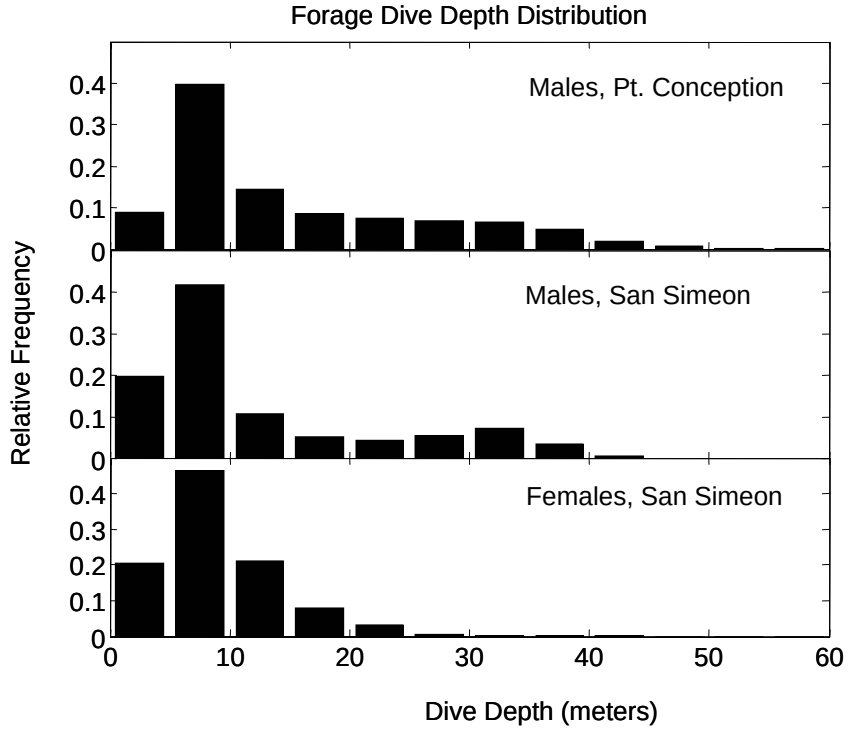

Figure 55. Frequency distributions of forage dive depths for three groups of study animals: males at Pt. Conception (top) males at the more northerly San Simeon study area (middle) and females at San Simeon (middle).

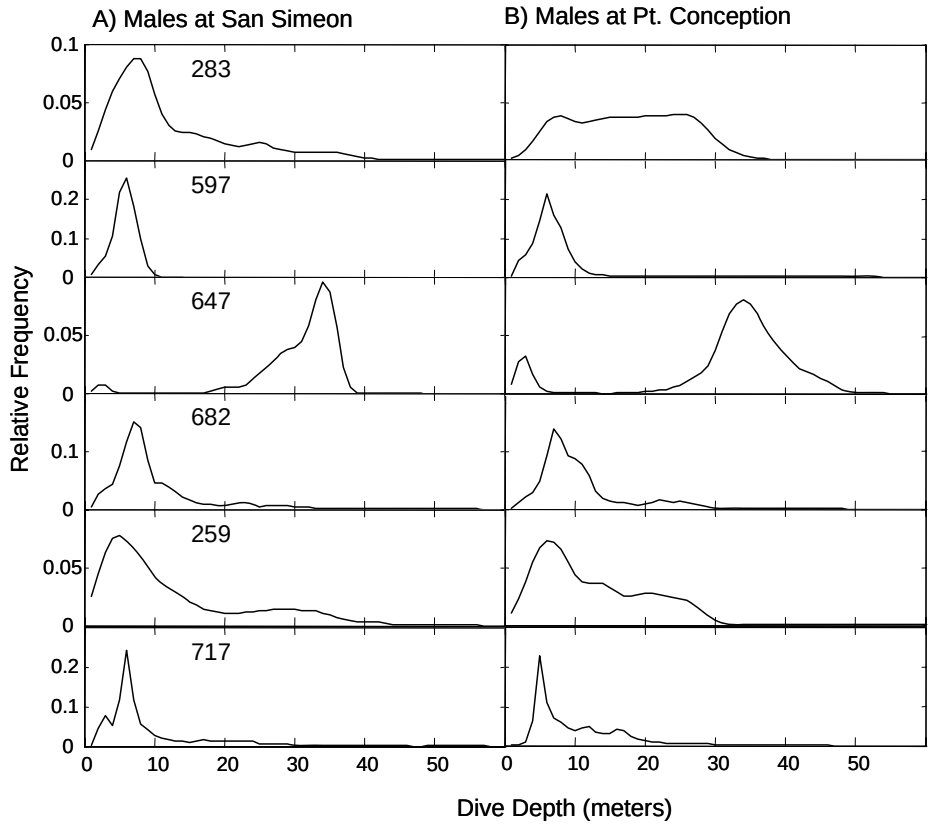

Figure 56. Frequency distributions of feeding dive depth (shown as non-parametric probability density curves) for individual male study animals during periods spent at San Simeon (left hand graphs) and periods spent at San Simeon (right hand graphs). Note that the left-hand and right-hand graphs in each row represent data from then same study animal.

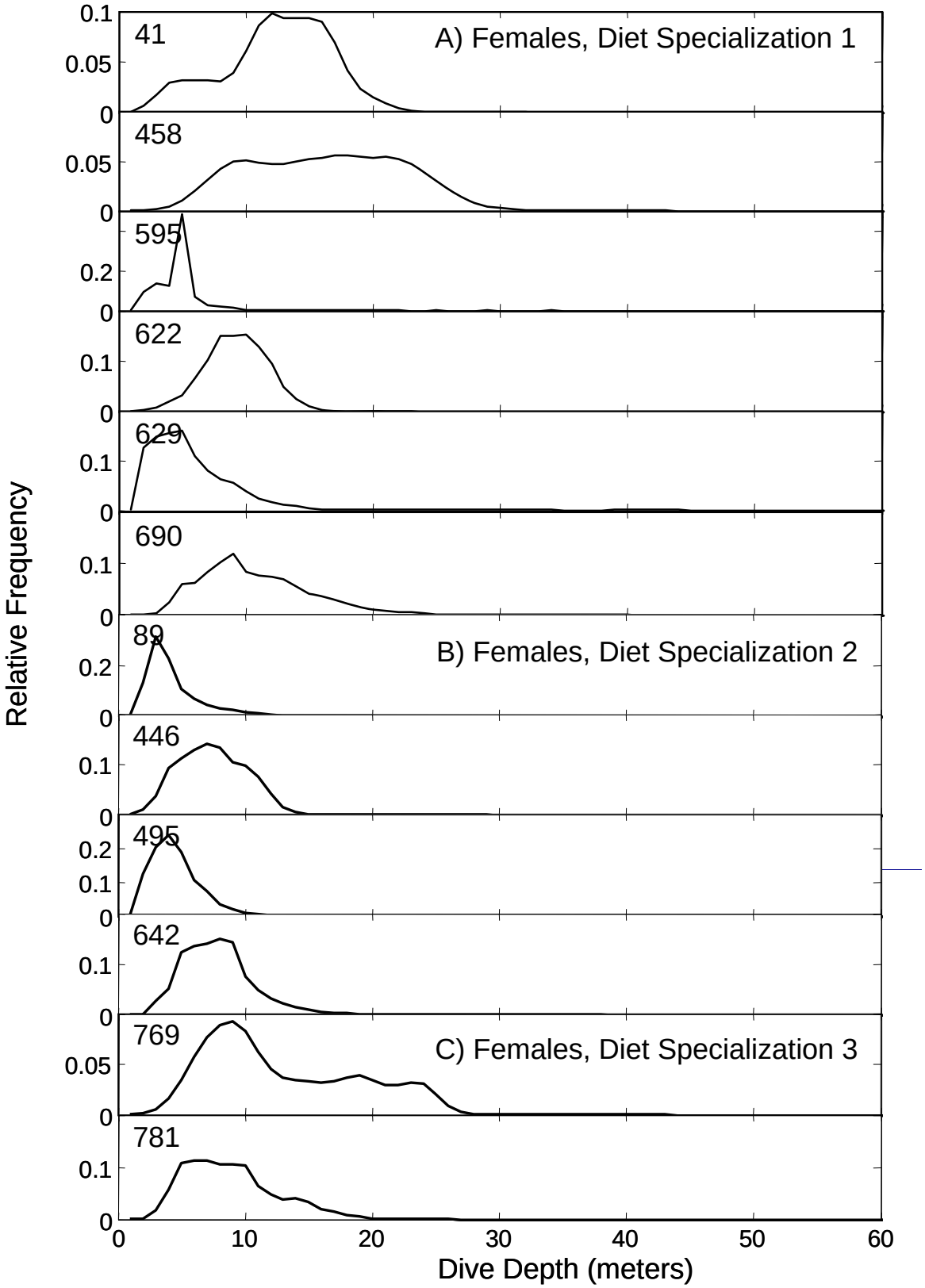

Figure 57. Frequency distributions of feeding dive depth (shown as non-parametric probability density curves) for individual female study animals. The top 6 graphs represent data from type-1 diet specialists, the 4 graphs below these represent data from type-2 diet specialists and the bottom 2 graphs represent data from type-3 diet specialists.

Mean foraging dive depth for males was slightly greater at Pt. Conception than at San Simeon, and depth distributions were found to differ significantly between the two study areas (KS = 0.130, P = 0.006; Figure 55). In the case of all 6 males that utilized both locations (Table 16), individual mean dive depths were greater at Pt. Conception than at San Simeon (14.9m vs. 13.4m, Wilcoxin P = 0.031), as was post-dive interval (66s vs. 55s, Wilcoxin P = 0.031), but there was no significant difference in dive duration (107s vs. 98s, Wilcoxin P = 0.244).

Classification by dietary specialization (as determined from direct foraging observations; Chapter 5) was possible for 12 of the 14 females, and there were marked differences in dive behavior between the three diet types (Table 16). Females that utilized type-2 diet specialization (intermediate-sized prey) tended to exhibit shallower and shorter dives than either type-1 (crab and abalone) or type-3 (snail) specialists (Figure 53 and Figure 57). Post dive interval also differed significantly between the three diet types (Table 16), and in fact a combination of mean and variance in post-dive interval could be used to reliably distinguish the three specialist types (Figure 58).

There was no difference in mean dive depth between day and night for females (Wilcoxin P = 0.2412, n = 14), but males tended to have slightly deeper dives in the day (mean = 14.4m) than at night (mean = 11.5m) (Wilcoxin P = 0.0273, n = 10). We found no significant differences between daytime and nighttime foraging dives by males and females with respect to dive duration (Wilcoxin P = 0.6257 and 0.3750, respectively) or post-dive interval (Wilcoxin P = 0.0906 and 0.4316, respectively).

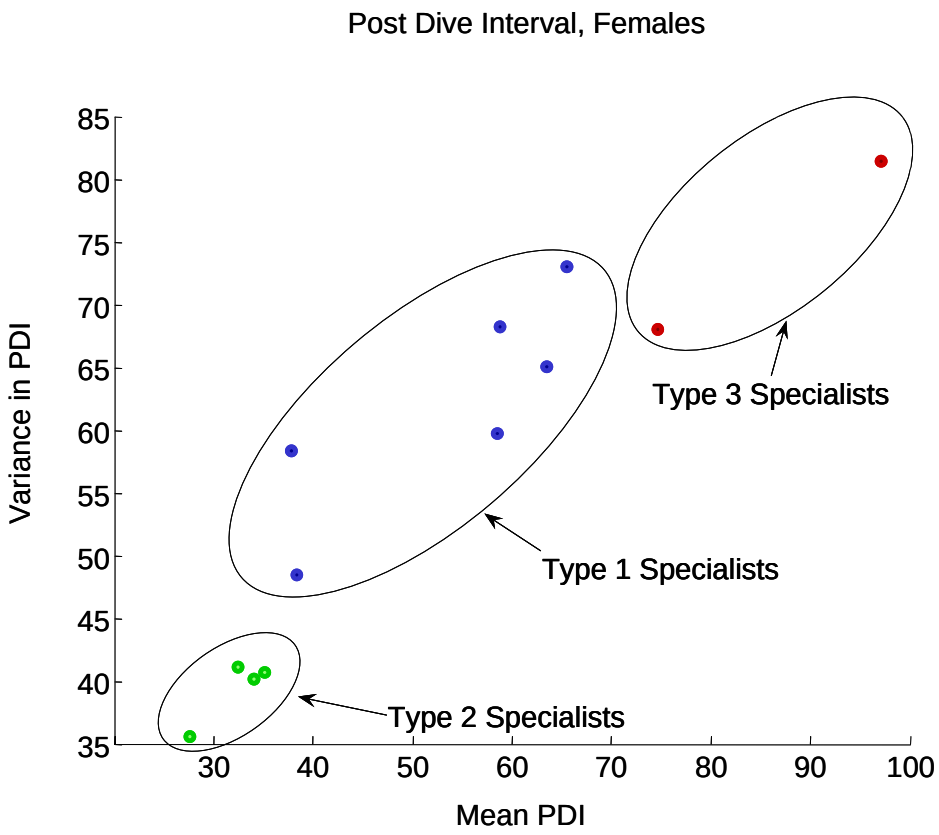

Figure 58. Plot of variance in post-dive interval vs. mean post-dive interval for 12 female study animals, showing consistent differences between the 3 diet specializations.

Activity Budgets

For 25 activity sessions having matching, independent estimates of percent time foraging, the telemetry-based method resulted in a mean estimate of 35.4% time feeding while the TDR estimate was 34.6%. The median difference between individual sessions was 0.09% and the mean difference was -0.08% (95% confidence interval for the mean = -4.73 – 3.13%). Although there was no indication of a prevailing bias between the two techniques, there was considerable variation in estimated activity budgets calculated for individual 10-hour periods, with differences ranging between -20 and 20% (Figure 59). It is unclear how much of this variation arises from one method or the other. Boot-strap analysis showed that variance attributable to individual variation reached an asymptote at approximately 20 individuals (Figure 60), suggesting that our sample size of 24 individuals should be fairly representative of population-level variation, although data from more individuals will be needed to confirm this. Activity budget estimates from TDR records provide more precise estimates for a given sample size (i.e. 3-12 continuous months of data for 24 animals), so we used this data set for remaining analyses.

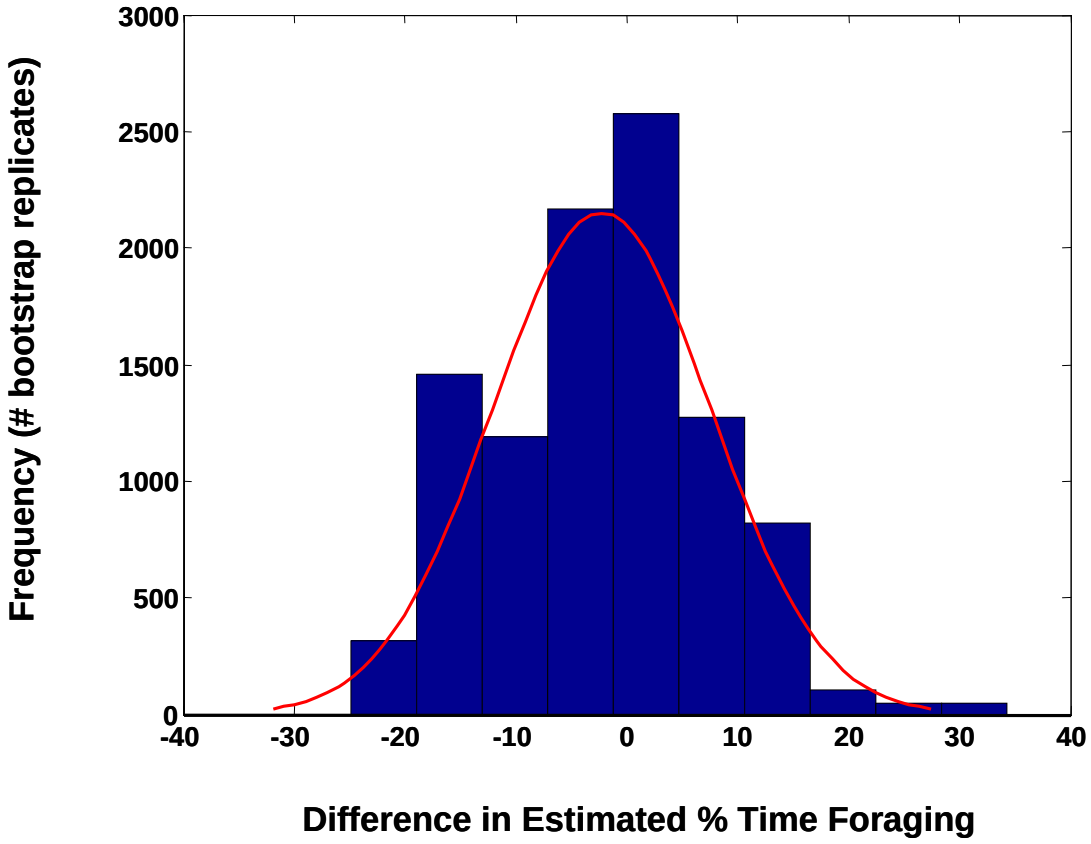

Figure 59. Frequency distribution of deviations between two independent estimates of percent time feeding for 10-hour periods (based on 10,000 boot-strap replications). A value of 0 on the horizontal axis indicates no difference in estimated percent time feeding as calculated from TDR data analysis or telemetry-based methodology (see text for explanation of these two methods). A normal probability density function was fit to the distribution and is plotted over the bars, indicating mean difference not significantly different from 0.

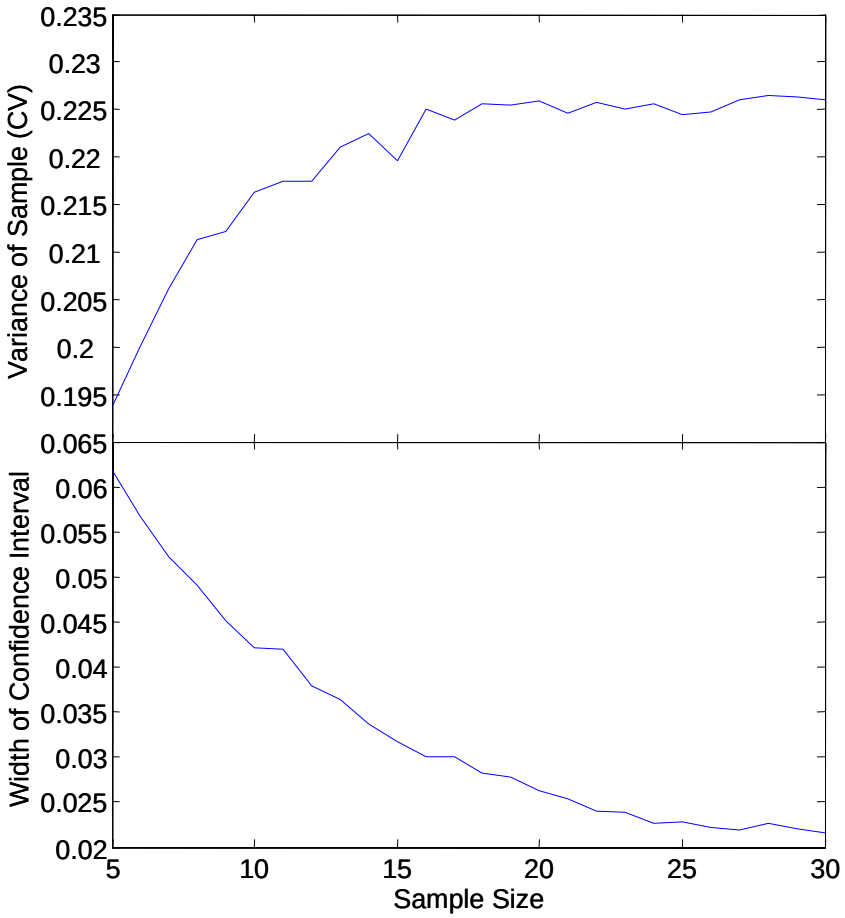

Figure 60. The potential effect of sample size (number of study animals) on activity budget estimates from TDR data are shown (based on boot-strap analysis of data from 24 study animals). The top graph shows the relationship between sample size and estimate variance, measured as the coefficient of variation; the bottom graph shows the relationship between sample size and estimate precision, measured as the width of the 95% confidence interval.

There was no significant difference in percent time foraging between spring, summer/fall and winter ($F = 1.39$, $P = 0.2603$), although there was a trend towards slightly less time spent feeding between August and October (Figure 61). There was considerable individual variation in diel foraging patterns: a few animals conducted up to 75% of their foraging during the day while a few other individuals conducted 75% of their foraging at night. At the level of the population, however, there was no net bias towards daytime or nighttime feeding: males conducted 48% of their foraging during the day (95% CI = 42–55%) while females conducted 51% of their foraging during the day (95% CI = 45 – 57%). Interestingly, type-3 diet specialists (snail feeders) tended to have a slightly higher proportion of feeding dives at night (56% at night, 95% CI = 51 – 63%), but there was no net bias for type-1 or type-2 diet specialists.

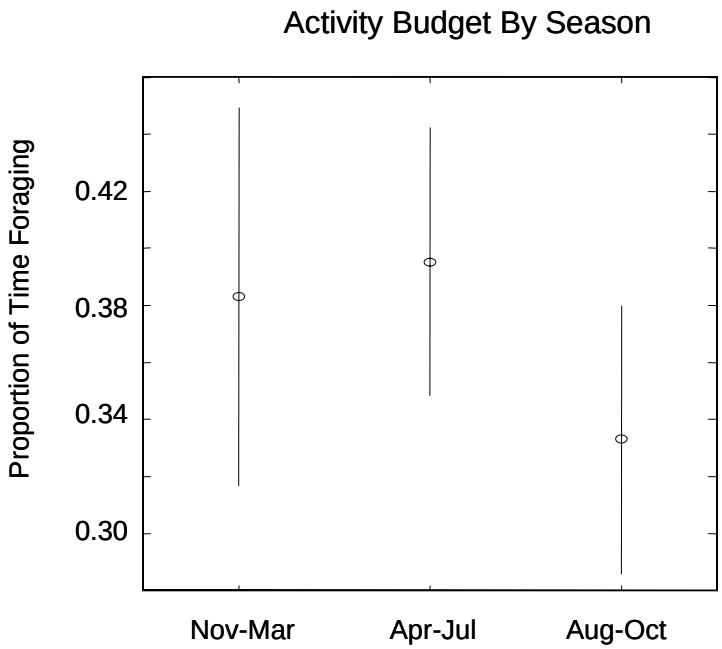

Figure 61. The mean proportion of time spent foraging by all study animals is shown for three seasons. Error bars represent 95% confidence intervals (differences between seasons are not statistically significant).

For each of the 5 males that spent extended periods of time (> 2 weeks) at both Pt. Conception and San Simeon there was less time spent foraging at Pt. Conception (Figure 62). No significant difference was found in the percent time foraging by females with or without a pup ($F=1.03$, $P=0.361$). Contrasting the telemetry-based estimates of percent time foraging by females and males in the present study with equivalent data from the 1980's (the 1980's values represent telemetry-based, average estimates), it appeared that the average percent time feeding for females had increased relative to the 1980's (Figure 63), although the variance associated with the telemetry-based estimates resulted in statistically non-significant differences. Examining the TDR-based estimates we found the same temporal patterns for females, but in this case the estimated percent time feeding was significantly greater in the present study than in the 1980's. The estimated percent time foraging by males also showed an increase relative to the 1980's (based on TDR estimates but not on telemetry estimates), although the difference was less pronounced at Pt. Conception (Figure 63).

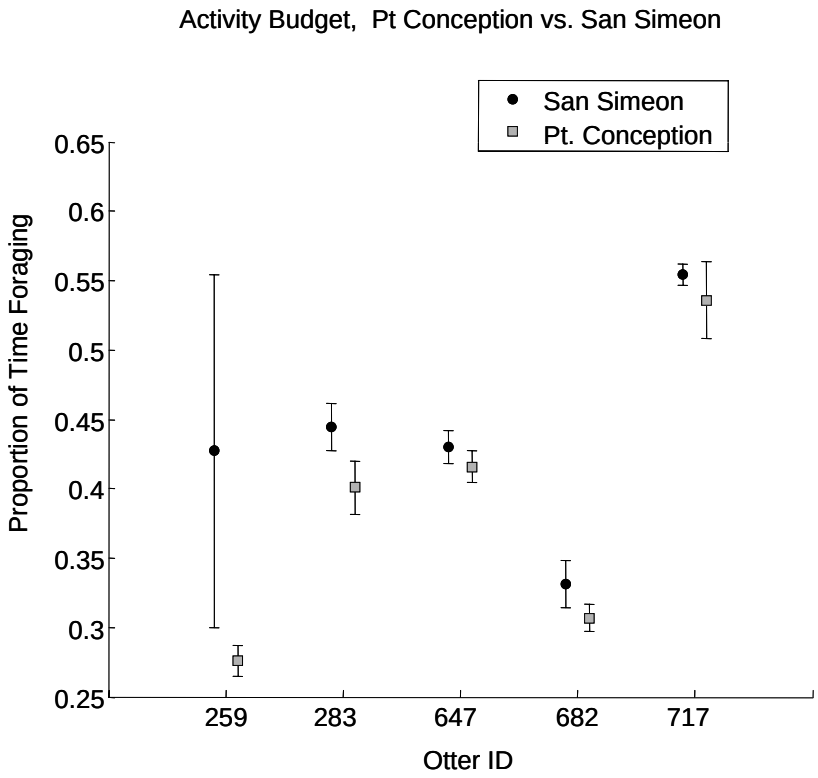

Figure 62. The mean proportion of time spent foraging at two locations by 5 male sea otters (un-ordered along the horizontal axis). Less time was spent feeding at Pt. Conception by each individual, although there were considerable individual differences in activity budget. Error bars indicate 95% confidence limits around the individual means.

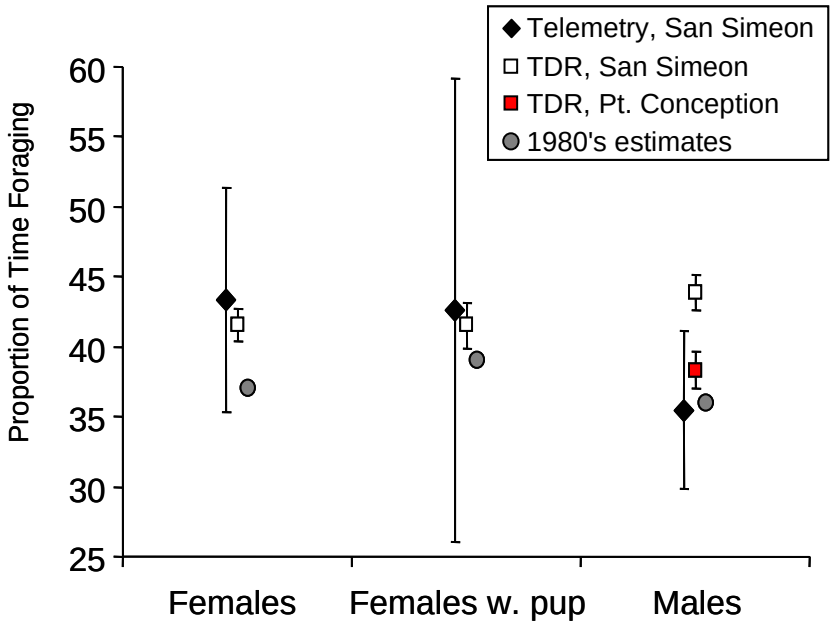

Figure 63. Temporal comparison of estimated proportion of time spent foraging by three groups of study animals, adult females without pups, adult females with pups, and adult males. Error bars indicate 95% confidence limits around the group means.

Discussion

Time-depth recorders provide a number of new and previously un-measurable quantities relevant to understanding habitat use and feeding behavior in sea otters. The most simple yet perhaps the most important quantity provided is the range of depths used for feeding, and the relative frequency with which various depths are used. Among other applications, this information can be useful for identifying critical foraging habitat for sea otters in different locations, which can subsequently be incorporated into management plans to mitigate potential conflicts between sea otters and human activities. The data presented here indicate that habitat use patterns vary among individuals and between locations (Figure 55 – Figure 57), and therefore it is important that data be collected from a sufficient number of individual animals of different age/sex classes and at different locations to ensure that a representative picture of the population is obtained. In the present study we have collected representative data from adult males and females, but future work will be needed to obtain data from juveniles and sub-adults, and from other locations within the range. Some of these data will be provided by ongoing work in the Monterey Bay area (J. Bodkin and M. Staedler, personal communication). However, it is important to remember that other habitat factors such as protected resting locations and areas suitable for pup rearing will be important in assessing habitat quality, and may not be reflected in TDR data alone.

Consistent with findings from Alaskan sea otters (Bodkin et al. 2004), it appears that females and males utilize different depth ranges for feeding (Figure 55). Research on sea otter diving physiology (Chapter 7 and 8, this report) will help to resolve whether this difference reflects a physiological constraint (i.e. females simply can't dive to the deeper depths utilized by males), or is an alternative solution to the problem of balancing energy costs and energy gains for a small diving mammal (e.g. Costa 1991). Interestingly, with very few exceptions both males and females tended to exhibit a peak of depth use in the 5–10m range, but most females showed only limited use of depths beyond this range, whereas males were more likely to exhibit a secondary peak of use at the 25–40 m depth range, similar to the bi-modal frequency distribution reported for Alaskan sea otters (Bodkin et al. 2004). More work will be needed to determine whether this secondary peak corresponds to a qualitatively different foraging strategy employed by these individuals (with respect to either dive behavior or prey selection).

It is becoming increasingly clear from studies of diving birds and mammals that the distinct foraging strategies used by different species are reflected by remarkably different patterns of dive behavior, each one adaptive in the context of a particular combination of prey abundance and distribution (e.g. Croxall et al. 1988, Costa 1991, Tollit et al. 1998, Tremblay and Cherel 2000, Costa and Gales 2003) . The relationship between foraging strategy and diving behavior was evident for sea otters in the characteristic differences between females with different dietary specializations (Figure 53 and Figure 58). We have found that consistent patterns of prey selection and handling technique allow the unambiguous classification of females into 3 distinct diet types (Chapter 5), and this classification scheme was further supported by the differences in dive depth, duration and especially post-dive interval (Table 16; Figure 58). The longer and more variable post-dive interval corresponds very closely to the observed surface handling times for each of the three diet types (Chapter

5), indicating that post dive interval may be of use for assessing forage success rates or diet specialization from TDR records in the absence of accompanying observational data.

The differences in dive behavior and time-activity budgets of male otters at Pt. Conception as compared to San Simeon are consistent with the hypothesis that males experience greater foraging success at the southern study area. The slightly deeper dive depths recorded at Pt. Conception may appear to contradict this conclusion because deeper dives are generally more costly (Costa 1991, Kooyman and Ponganis 1997); however, dive depth alone is probably a poor indicator of foraging success. Indeed, Bodkin *et al.* (2004) concluded that male sea otters in SE Alaska experienced greater prey abundance at deeper depths, thus counter-balancing the additional costs associated with deeper dives. A more significant difference between the two locations was the longer and more variable post-dive interval for feeding dives at Pt. Conception (Table 16), suggestive of a higher rate of prey capture and/or larger individual prey items. Individual males also devoted less time to feeding at Pt. Conception, suggesting they mere able to meet their metabolic demands faster at this location. Due to the limited sample size and the paucity of direct foraging observations from Pt. Conception, it is unfortunately not possible to rigorously test this hypothesis; however, the data reported here for 6 males is at the very least suggestive, and is also consistent with all the other information collected from the Pt. Conception study animals (greater relative body size, better survival rates, etc.).

One very encouraging result of our analyses was the concurrence between estimates of time-activity budgets derived from two independent techniques (Figure 59). A combination of visual observation and radio-telemetry data has provided field biologists with reliable estimates of sea otter activity budgets for over 20 years (Loughlin 1980, Garshelis et al. 1986, Siniff and Ralls 1988, Ralls and Siniff 1990, Ralls et al. 1995, Tinker and Estes 1996, Gelatt et al. 2002), the one chief drawback of this method being the extensive effort required to achieve a fairly small sample size. Our results suggest that the use of TDR data can largely rectify this by providing vastly increased sample sizes for each individual animal. It is important to note, however, that the increase in precision applies to data from individual animals; the high degree of intraspecific variation still requires a relatively large and representative sample of study animals if one is to obtain a representative measure of population status. Sample sizes much smaller than our current sample of 24 animals will likely result in less precise estimate of activity budget and/or will fail to capture the full range of variation in the population (Figure 60).

It appears that sea otters in the present study devoted more time to foraging than sea otters in the 1980's, based on a comparison with the mean estimates from the 1980's study (Ralls and Siniff 1990). This finding is consistent with the apparently low rate of energy input that was estimated based on foraging observations (Chapter 5), and indicates that otters in the center of the range have modified their activity to adjust to increasingly limited food resources. The precise extent to which sea otters are capable of increasing their foraging effort has yet to be determined, although an upper limit must ultimately be set by basic physiological sleep requirements. Our results suggest that the periodic movements of some males to and from Pt. Conception, where food appears less limiting, may represent an alternative solution to the problem posed by limited food resources in the center of the range. The relationship between sea otter densities and population status (with respect to food resources) has proven

difficult to describe in California, largely because of the complex interplay between the diverse mortality factors that seem to limit population growth in this population (Estes et al. 2003a, Kreuder et al. 2003, Gerber et al. *in press*). Intra- and inter-population comparisons of time budgets and foraging behavior provide one of the most promising approaches to understanding this relationship (Bodkin and Ballachey 1996), and the use of TDR's will greatly improve our ability to measure these key parameters.

Chapter 7. Thermoregulation and diving energetics

Laura Yeates, Terrie M. Williams, M. Tim Tinker and James A Estes.

Abstract

1. For all animals, body maintenance, activity and reproduction require expenditure of energy. Sea otters are small marine mammals that live in water temperatures that are up to 30ºC lower than their body temperature, and temperature regulation may be a major factor determining overall energy costs to individuals.
2. We measured core body temperature (T_b) in radio-tagged sea otters from San Simeon to Point Conception, California, using temperature sensitive VHF radio transmitters and a scanning receiver equipped with a special computer interface that records date, time and body temperature at one minute intervals.
3. We also measured energy expenditure in two adult male California sea otters while resting, diving, foraging and grooming in a 9.1m deep tank at Long Marine Laboratory seeded with live prey.
4. Study animals exhibited a highly variable body temperature. Temperature frequently varied up to 2ºC within a 24hr period. There was a strong relationship between behavior and body temperature. Resting periods lasted only until the heat produced by processing food diminished. Otters were not observed resting unless they had foraged beforehand. This strongly suggests that otters depend on the heat increment of feeding (HIF) for supplementing their thermal budgets and must digest food in order to rest for prolonged periods.
5. We estimated the daily energetic requirements for individual wild otters based on observed activity budgets, in conjunction with data on metabolic rates measured in the laboratory and augmented by published values.
6. The highest energetic cost was associated with grooming after feeding. Although costly, grooming is clearly necessary for effective thermoregulation.
7. Adult males had particularly high daily energetic requirements as compared to adult, non-lactating females, and this was attributed both to greater body size and to the higher proportion of time spent swimming at the surface. Their high energy demands imply that limited food resources will impact adult males disproportionately, which may help to explain their frequent long-distance movements to the south end of the range where food is more abundant.
8. These results suggest sea otter activity patterns are shaped in large degree by thermoregulatory requirements. Also, although the high energy demands of sea otters can be offset by increased foraging effort to some degree, activity budgets are also constrained by thermoregulatory requirements, and thus periodic migration to areas of higher food abundance may be an alternative solution to energetic shortfalls.

Introduction

Among mammals, sea otters represent the most recent lineage to reenter the marine environment (Berta & Sumich 1999). While pinnipeds and cetaceans have maintained aquatic lifestyles for over 50-60 million years, sea otters have been fully aquatic for only 1-3 million years. As a result, sea otters lack many of the more derived aquatic adaptations of cetaceans and pinnipeds. It follows that these small mammals have retained many of their ancestral terrestrial characteristics. The implication is that aquatic living may be especially challenging for sea otters when compared to other marine mammal species.

One of the biggest challenges upon entering the marine environment for any mammal is the maintenance of a stable, high, core body temperature while immersed. The thermal conductivity of water is ≥ 25 times that of air (at the same temperature) resulting in high levels of heat loss (Schmidt-Nielsen 1997). Sea otters use several mechanisms to offset high heat loss including: (1) an efficient method of insulation (Williams et al. 1992); (2) a comparatively high metabolic rate to terrestrial mammals of similar size (Morrison et al. 1974, Costa and Kooyman 1984, Williams 1989); (3) an increase in time spent active over a 24hr period, and (4) utilization of supplemental heat produced by digestion known as the heat increment of feeding (HIF) (Costa and Kooyman 1984). These traits are highly interrelated and act in concert to maintain a stable core temperature. However, in most cases these mechanisms have only been measured in a laboratory setting.

For sea otters, insulation is provided by an air layer trapped against the skin by the fur (Williams et al. 1992). Although the conductance of fur is comparable to blubber of the same thickness, fur cannot function as an energy store, an added benefit provided by blubber. In addition, air is compressed out of the fur as the otter dives, thereby reducing the insulative quality of the fur at depth. Sea otters also have a remarkably high metabolic rate (2.8 times that of a terrestrial mammal of similar size, Morrison et al. 1974, Costa and Kooyman, 1982), even when compared to other marine mammals. Weddell seals (*Leptonychotes weddellii*), bottlenose dolphins (*Tursiops truncatus*), and California sea lions (*Zalophus californianus*) have metabolic rates 1.5-2 times that predicted by Kleiber (1975; Castellini et al. 1992, Williams et al. 1993, Hurley and Costa 2001, Williams et al. 2004). Presumably, this elevated metabolism aids in thermoregulation for this small mammal, although not without obvious energetic costs.

Despite these mechanisms for mitigating heat loss, sea otters have a narrow range of water temperatures in which they are able to maintain a stable core temperature without increasing metabolism known as the thermal neutral zone (TNZ). Thermal neutral range of water temperatures for sea otters spans only 5ºC (20ºC to 25ºC) (Morrison et al. 1974, Costa and Kooyman 1984). In comparison, cetaceans have thermal neutral zones that may extend over 15 to 20ºC ranges (Williams et al. 2001). Such a narrow thermal neutral zone undoubtedly represents a thermoregulatory challenge to the sea otter. Ambient water temperatures range from 0 to 19ºC from Alaska to California. Consequently, sea otters spend the majority of their lives in water temperatures outside their thermal-neutral zone, a pattern rarely seen among marine or terrestrial mammals (Scholander et al. 1950).

All of the thermoregulatory mechanisms used by sea otters are inherently labile. As a consequence, not only are body temperatures variable, they can change over a relatively brief period of time. For example, even partial soiling of the pelage during an oil spill can reduce the insulative quality of the fur dramatically and instantly (Costa and Kooyman, 1982). In view of the mismatch between the sea otter's thermal neutral zone and the temperatures typically encountered in the wild, and in view of the dynamic nature of the mechanisms it uses for thermoregulation and the lack of substantial energy reserves with which to offset periods of elevated energetic demands, it is reasonable to hypothesize that sea otters must have high daily energetic requirements and above-average vulnerability to environmental or ecological perturbations.

We studied the relationship between body temperature, behavior and activity in wild sea otters along the California coast from San Simeon to Point Conception. Additionally, we measured the oxygen consumption in two captive adult male sea otters while performing behaviors observed by otters in the wild. We combine these data to estimate the daily energetic needs in sea otters, and we discuss the potential consequences of behavioral changes under conditions of limited prey availability.

Methods

Study Animals

Techniques and study design for the capture, instrumentation and monitoring of sea otters are described elsewhere in this report (refer to Chapters 1, 2 and 9 for details). Thirty six of the 72 study animals (10 males, 26 females) were selected arbitrarily for measurements of core body temperature. The abdominally implanted radio tags used in this study provided real time measurements of core body temperature of the animal based on pulse rate of the radio signal. Each tag was calibrated in a water bath over a range of expected core temperatures prior to implantation.

Two adult male sea otters were transferred from Monterey Bay Aquarium's Sea Otter Research and Conservation Program (SORAC) to California Department of Fish and Game's Marine Wildlife Veterinary Care and Research Center (Santa Cruz, CA) to be used for measurements of energy expenditure. The otters were maintained in two sizes of outdoor fiberglass holding pools, 4.2m diameter, 1.2m deep and 6m diameter, 1.5m deep. Fresh sea water was continuously added at a minimum of 15.5 lpm (60gpm). Water temperature varied with ambient ocean temperature (10 to 19ºC).

Core body temperature and behavioral measurements

Twenty-four hour observation sessions were conducted on each wild otter following the methods of Loughlin (1980) and Ralls and Siniff (1990). Activity was determined by direct observation and based on readily distinguishable characteristics of the temporal pattern of the transmitted radio signals, thus making it possible to measure activity patterns and time budgets during the hours of darkness. Other information recorded included date, time-of-day, location, sea-state, weather conditions, air and water temperature, duration of the

surface interval and submerged interval for each feeding dive, number and species of prey captured and size of prey items (during daylight hours only) following the methods of Ralls *et al.* (1995).

Behaviors were classified as resting, foraging, or other (grooming, surface swimming and reproductive behaviors). Resting meant that the otter was inactive, floating on the surface of the water. Foraging consisted of diving, obtaining prey and consuming it at the surface. Grooming was defined as the otter rolling, somersaulting, vigorously rubbing and pleating the fur. Short periods of time when the otter was out of sight and the radio signal was lost were classified as "behavior unknown".

All analyses were limited to adult males and adult non-lactating females. Only 24-hour activity budgets with less than 10% of the day classified as unknown were used for calculating mean core body temperatures. Analyses of the change in temperature during behaviors were limited to behavior bouts where body temperatures from start to end of the bout were available. The resulting dataset was used to derive summary statistics on core body temperature, activity patterns, and the relationships between these two variables.

Body temperature profiles from a sub-set of study animals with the most complete data sets (4 adult males) were analyzed in greater detail to test for association of temperature fluctuations with behavioral changes. A sample of 20-minute time intervals were selected and classified as either constant temperature (variation < 0.2°C) or temperature peak/trough (variation > 0.4°C). We sampled a total of 52 intervals, half of them constant and half of them classified as peak or trough. We then scored each interval based on whether or not there was a change of activity state during the interval, and a Pearson Chi-square contingency test was used to test the null hypotheses of no association between behavioral changes and temperature peaks or troughs.

Oxygen consumption

Energetic measurements were made using two captive adult male otters that were trained to make voluntary dives and then surface beneath a floating Plexiglas dome, allowing metabolic rate to be measured via indirect calorimetry (i.e. via rate of oxygen consumption). Prior to all experiments, captive otters were fasted a minimum of 12 hours. All measurements were made using an open flow respirometry system (Sable Systems International, Henderson, NV). Briefly, a sub-sample of dome exhaust was drawn through a series of three columns filled with Drierite and Baralyme before entering the oxygen analyzer (model FC1-B, Sable Systems, Henderson, NV). Air was pulled through the dome at a rate of 180-190 L min^{-1} by a mass flow meter (Flow kit 500H, Sable Systems, Henderson, NV). Oxygen content of the dome exhaust and flow rate were logged every 2.0 second on a laptop computer. The oxygen content of the dome remained above 20.3% for all trials. Gas contents were corrected to standard temperature and pressure (STPD) and converted to oxygen consumption using the equations of Withers (1977).

All diving trials were conducted in a 9.1m deep sea water storage tower. Otters were monitored through an underwater video camera mounted inside the tank. A rocky substrate and live rock crabs (*Cancer* spp.) were added to the bottom of the tank to simulate foraging

conditions in the wild. Otters were placed in the tank and allowed to forage on live prey, making repeated dives to the bottom to collect prey items and then surfacing beneath the dome to handle prey. Otters were removed from the tank after they had consumed all prey or had stopped foraging on their own. Foraging bout duration ranged from 60 to 145 minutes. Foraging metabolic rate was calculated using one foraging bout per otter under similar conditions (i.e. time of day, water temperature and number of prey on the bottom were standardized), and only dives where the otters were visible during the entire dive were included in the analysis.

Daily energy requirements for individual study otters were estimated by combining the field-measured activity budget with estimates of activity-specific metabolic rate, as measured in captive trials and supplemented with data from Williams (1989). Oxygen consumption rates were converted to caloric requirements (kcal/kg) for comparison with energetic input from foraging (see Chapter 5, this report). To compare males and females, mass-specific caloric requirements were used.

Statistical analysis

Statistical analyses were performed using SYSTAT 10.2 (Systat Software Inc. Richmond, CA). All results are reported mean ± 1 standard deviation. Multiple comparisons of independent samples were made using a single factor ANOVA, unless otherwise stated, and we report only P, the probability that the observed effects could occur be attributable to random sampling effects. We set the type-I error rate for all tests to $\alpha = 0.05$.

Results

Core body temperature and behavior

Sea otter body temperatures were not constant over time (Figure 64). Core temperature could fluctuate up to 2.3ºC within a 24-hour period. The overall mean body temperature of sea otters was 38.1 ± 0.3 ºC (n = 36). The mean body temperature for male otters was 38.4 ± 0.4 ºC (n = 10). Female mean body temperature was 38.0 ± 0.3 ºC (n = 26). Male and female mean core body temperatures were statistically different (P = 0.007). Within individual comparisons of day versus night body temperatures were made by using paired t-tests. There was no significant difference in mean resting body temperatures between day and night within individuals (for all individuals P > 0.05).

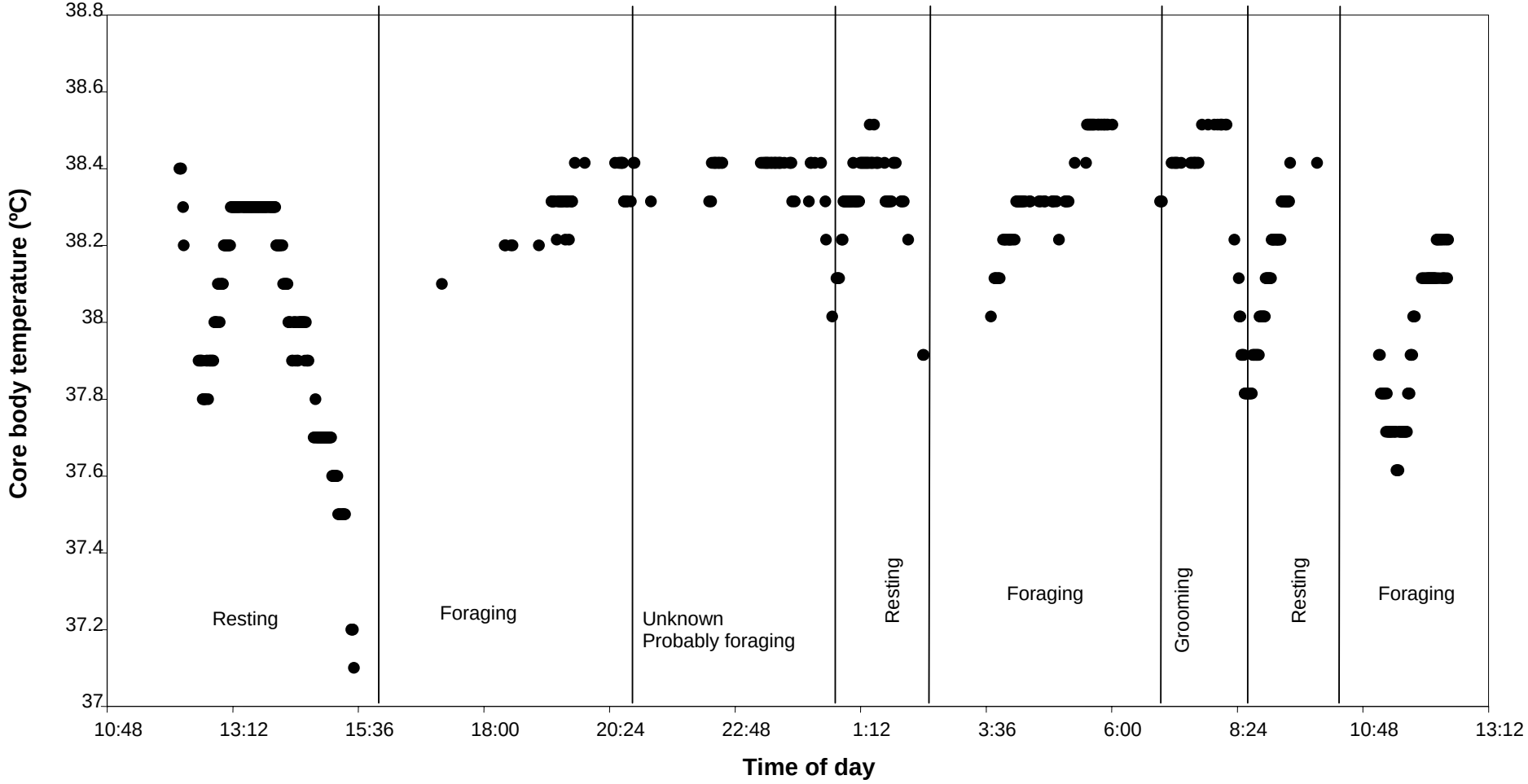

Figure 64. Representative profile of core body temperature of an adult male sea otter in relation to behavior and time of day. Each point represents the average core body temperature every 60 seconds. Corresponding behaviors are listed under the body temperature. Notice the pattern in temperature change over time for the same behaviors and change in behavior at temperature troughs

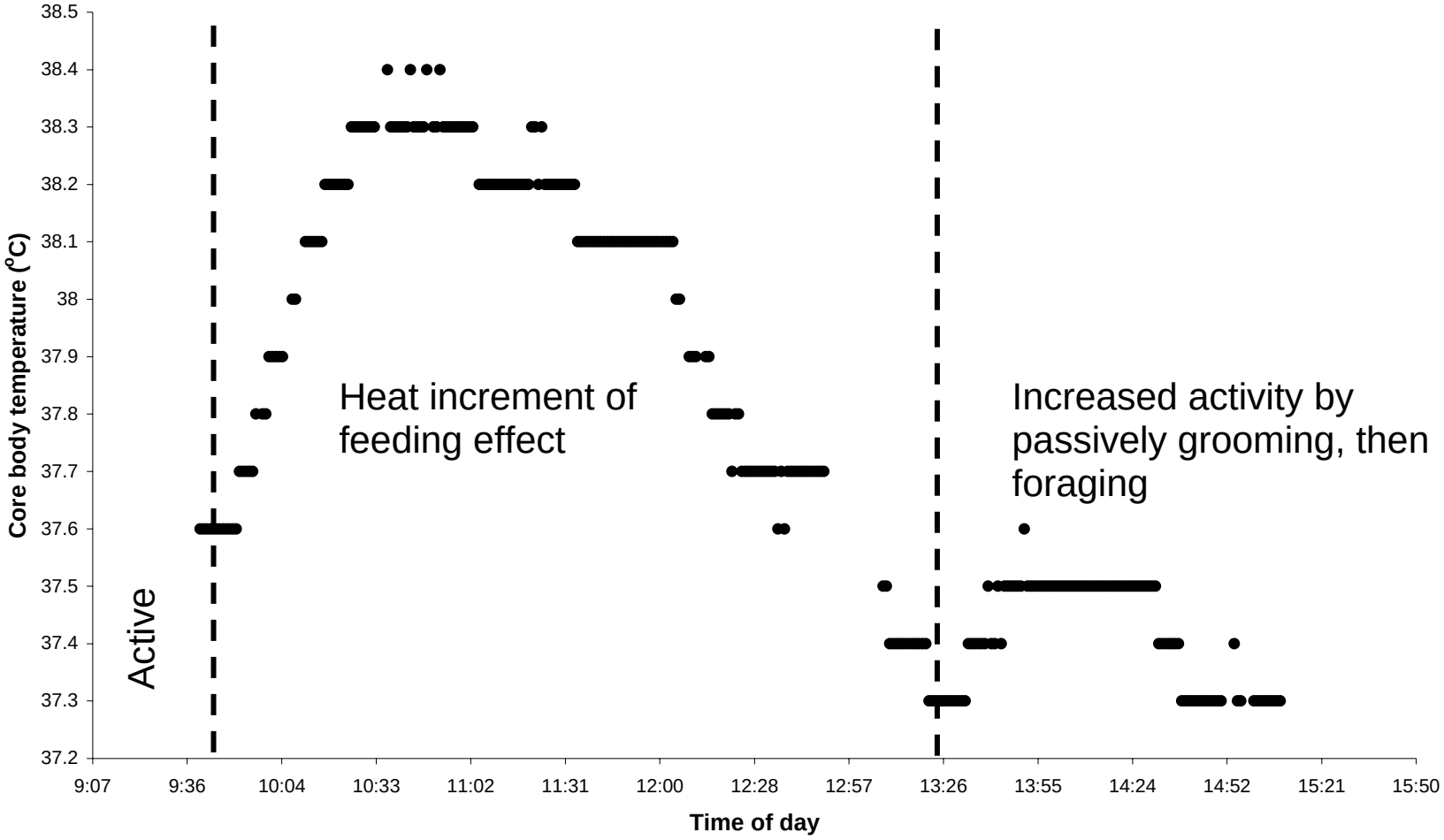

Figure 65. Representative core body temperature profile following a foraging bout of a male otter. Activity increased once the otter body temperature dropped to 37.3ºC.

For resting periods following foraging bouts, body temperature initially increased at an average rate of 0.9 ± 0.3ºC/hr, but this was followed by a decrease in body temperature at a mean rate of 0.6 ± 0.08 ºC/hr (n = 19) (Figure 65). Although there was no significant relationship between the amount of time spent grooming during a single grooming bout and net change in body temperature (Linear regression $R^2 = 0.15$, n = 30), there was a tendency for body temperature to decrease with time within a grooming bout (Linear regression $R^2 = 0.33$, n = 26; Figure 66). Peaks and troughs in body temperature tended to be strongly associated with changes in activity (Chi-square = 16.9, d.f. = 2, P <0.0001).

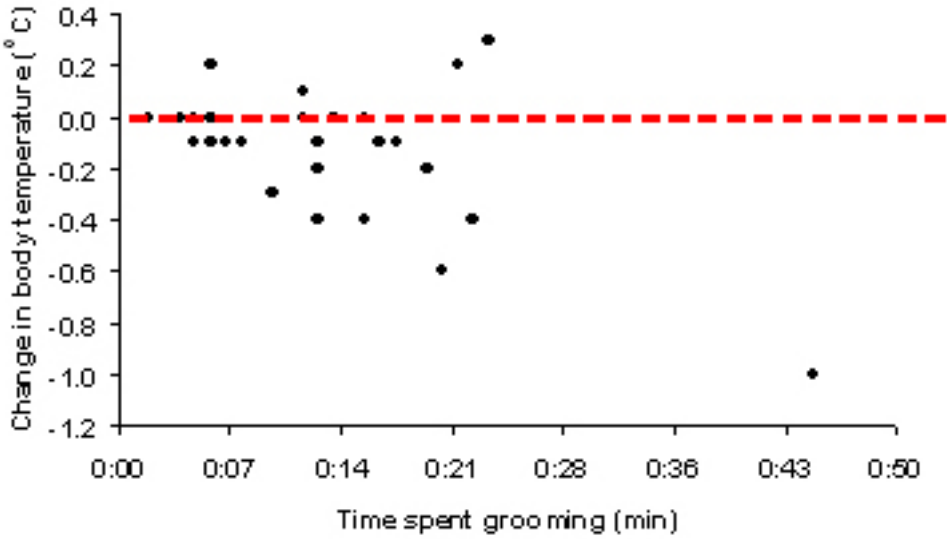

Figure 66. Change in body temperature for adult males during single grooming bouts. The dotted line denotes no change in body temperature.

Energetics

All metabolic experiments were conducted on different days, and for the purpose of this study, separate trials are assumed to be independent data points. Metabolic data were compared between the two study animals and no differences were found (P = 0.69), consequently we pool data for both animals.

No relationship was detected between water temperature and resting metabolic rate (temperature range = 13–17 ºC, $R^2 = 0.09$). Mean resting metabolic rate was 14.9 ± 2.0 $mlO_2\ min^{-1}kg^{-1}$ (n = 35) and was similar to published values (Morrison et al. 1974, Costa and Kooyman 1982, Williams 1989). Grooming (post prandial) incurred the highest metabolic rate, (29.4 ± 2.6 $mlO_2\ min^{-1}kg^{-1}$, n = 11; Figure 67). Mean foraging metabolic rate was 19.7 ± 2.9 $mlO_2\ min^{-1}kg^{-1}$ (n = 25; Figure 67). Metabolic rates differed significantly between all three activity states (P < 0.001).

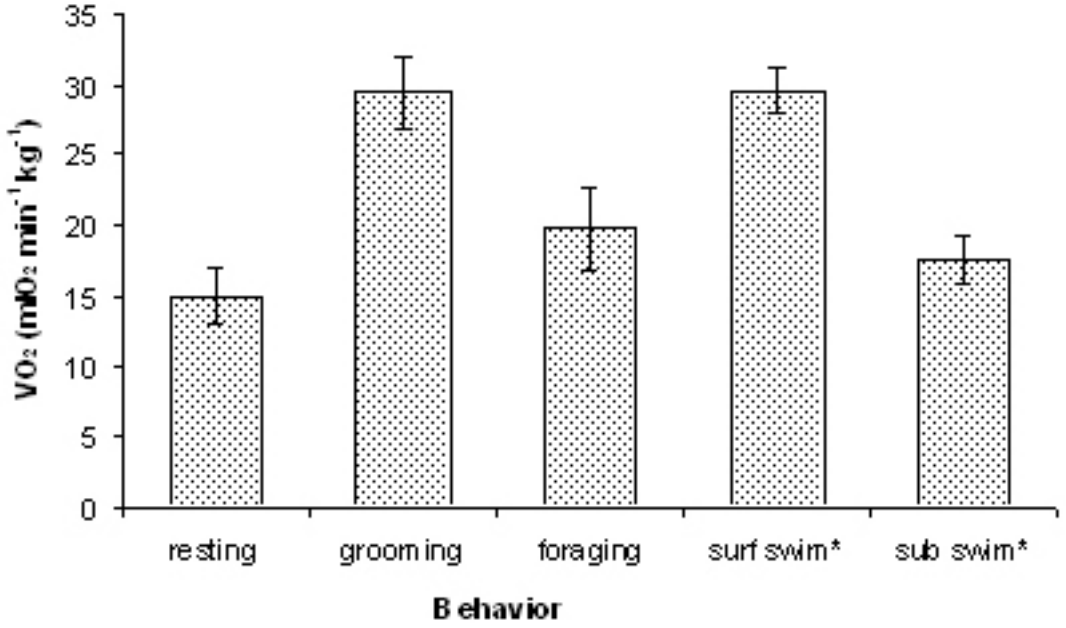

Figure 67. Mean metabolic rates measured in oxygen consumption for behaviors. Bars represent ± 1 standard deviation. Behaviors denoted with * are from Williams (1989).

For males, the mean estimated daily energetic requirement assuming an average activity budget (as described in Chapter 6, this report) was 3831.0 ± 709.2 kcal, while for females it was 2102.3 ± 489.2 kcal. The average mass-specific caloric requirement for females was 104.2 ± 25.8 kca/kg^{-1}, as compared to 126.4 ± 24.4 kcal kg^{-1} for males. There was a significant difference between the daily caloric requirements on a per kilogram basis between males and females (P = 0.028; Figure 68).

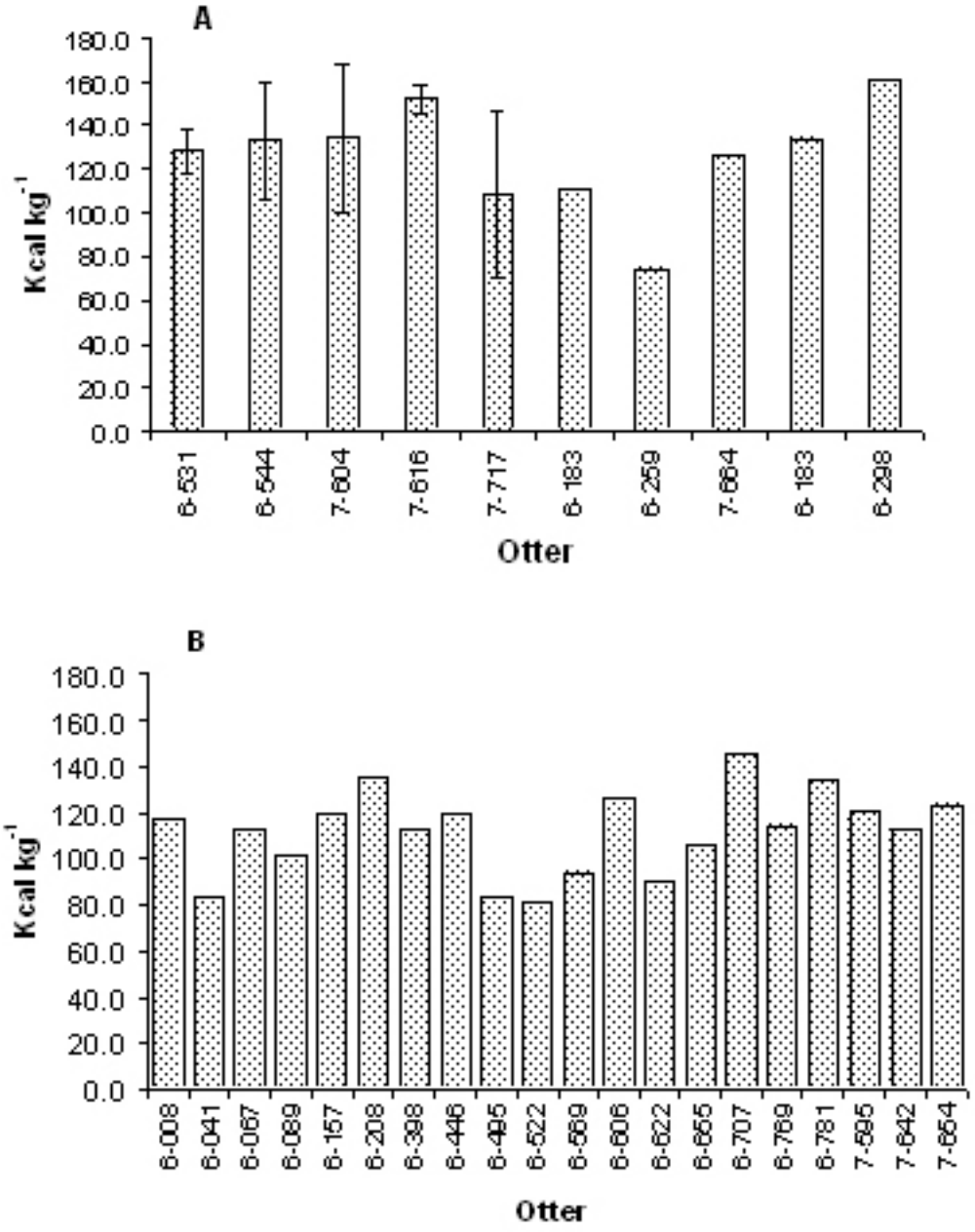

Figure 68. Estimated caloric requirements per kilogram for individual male (A) and female (B) otters. Individual otters are identified on the x-axis by otter number. The mean caloric requirement was calculated for otters with more than one activity budget. Bars indicate ± 1 standard deviation.

Discussion

Core body temperature and behavior

The otters in our study had an average temperature of 38ºC, which falls within the range of most eutherian mammalian body temperatures (Schmidt-Nielsen 1997). However, they showed highly dynamic core body temperatures (changes >2°C) over remarkably short periods of time (minutes). The physiological implications or costs of such rapid core temperature variation are as yet unknown, but such variability might have the benefit of reducing net thermoregulatory costs.

Core body temperature was clearly impacted by behavior, and this was seen most dramatically in the change in body temperature during post-prandial resting periods. Immediately following a foraging bout, otter body temperature followed a typical pattern, increasing at a high rate for the first portion of the resting bout, and then slowly decreasing over the subsequent period. Otters appeared to become active once body temperature had declined by more than 1–2°C from peak post-absorptive body temperature, presumably to offset the energetic cost of elevating body temperature by supplementing the thermal budget through the heat produced by exercise (Figures 65 and 66). Based on our observations, resting periods were invariably followed by foraging bouts. This temporal sequence of events closely matched that reported during laboratory-based oxygen consumption experiments by Costa and Kooyman (1984).

Otters did not show a decrease in body temperature during foraging bouts, as expected, and in fact we observed a mean rise in temperature of 0.2ºC. There are potentially three factors influencing body temperature during foraging bouts. The first of these is net conductance: as an otter dives the air is compressed out of the fur, likely reducing its insulative capability and increasing the rate of heat loss. Secondly, intrinsic heat production increases as a function of the exertion of feeding dives. Finally, digestion of ingested food (HIF) should also increase heat production as the foraging bout progresses. We had speculated that the longer the foraging bout or number of serial dives, the greater the increase in conductance, and we therefore had expected that body temperature would decrease after prolonged foraging until the resulting thermoregulatory costs brought an end to the bout. This expectation was not supported by the data, which suggest that foraging bout length is not limited by thermoregulatory demands; however, otters were often observed grooming between sets of dives, and these mid-bout grooming periods may serve to restore the air layer in the fur and thus extend foraging bouts. It appears that some other factor, such as muscle fatigue or gut capacity, is more important in limiting bout length. Interestingly, male otters did show an overall decrease in body temperature during grooming periods (Figure 66), a behavior that is critical to maintaining a clean pelage and thus a stable body temperature.

Energetics

Our overall estimated daily caloric requirements are conservative and should be considered a *minimum* daily requirement. For instance, because RMR was measured during post absorptive periods, it is likely an underestimate of resting metabolic rate because wild otters appear to rest only after foraging. Resting metabolic rate changes as food is processed, and

can be as much as 102% above post absorptive values (Costa and Kooyman 1984). Even though foraging experiments were set up to mimic biotic conditions in the ocean (rocky substrate, live prey) they did not simulate abiotic conditions such as waves or currents that otters would experience while diving, which likely increase the amount of energy expended during foraging. Regardless, otters showed high metabolic rates while performing normal sea otter behaviors during experimental trials.

Wild adult males had particularly high daily energetic requirements as compared to adult, non-lactating females, which was attributed in part to their greater body size (mean weight of males is 26.5 ± 2.9kg vs. females 18.0 ± 2.3 kg). Once the effect of body size was removed males still showed a significantly higher energy requirement than females. This appears to be a primarily a consequence of the increased time spent swimming at the surface (Williams 1989, Figure 68, Table 18). Most of the males included in this analysis were territorial, which means a substantial proportion of their daily activity budget was devoted to patrolling their territory (a "patrolling" male typically swims at the surface, ventral side down, with nose extended) and interacting with females. This stereotypical territorial male behavior is relatively expensive energetically, but these costs would not be incurred by non-territorial males, and presumably would not be incurred by these males when they were absent from their territories (i.e. when they moved to all-male aggregate areas such as Pt. Conception).

Table 18. The estimated daily energetic requirements for male otter 6-544 with different proportions of the day spent feeding, resting and other followed by the corresponding calories used to perform those behaviors. Note the increase in caloric need as percent time spent in "other" behavior increases. Metabolic rate estimate for "other behavior" represents the mean value for surface swimming, submerged swimming and grooming.

6-544

Feeding	Resting	Other	F_KCAL	R_KCAL	O_KCAL	DAY_TOT
22.39	52.24	25.37	947.0	1319.3	1577.8	**3844.1**
31.34	53.73	14.93	1325.9	798.2	928.1	**3052.2**
35.56	24.44	40.00	1504.1	973.2	2487.3	**4964.6**

Conclusions and Future Directions

Our results suggest sea otter activity patterns are shaped in a large degree by thermoregulatory requirements. Resting periods and possibly grooming periods may be constrained by changes in body temperature, although foraging bout duration did not appear to be so restricted. These thermoregulatory constraints have important implications for sea otter energy budgets. It has been well established that when sea otter populations encounter reduced food availability, their high energetic requirements tend to be offset by increased time spent foraging (Chapter 6, this report, Estes et al. 1986, Estes 1990, Gelatt et al. 2002). However, our data suggest that foraging effort is by no means an "unconstrained variable" for a sea otter, but rather may be tightly constrained by the requirements of temperature regulation. If this is the case, then the periodic migration by some territorial males to areas of higher food abundance (such as Pt. Conception) may represent an alternative solution to meeting energetic shortfalls. Although the actual travel between Pt. Conception and their regular territories is undoubtedly costly (Table 19), the increased rate of food consumption at

Pt. Conception, coupled with energy saved by not having to patrol territories, probably far outweighs these costs.

Table 19. Estimated daily energetic requirements for adult non-lactating female, an adult male and a traveling adult male with the same body mass. The activity budget for the adult traveling male is hypothetical. [1]Surface swimming and subsurface swimming are from Williams (1989).

18kg Female

Behavior	MR mlO_2 $min^{-1}kg^{-1}$	proportion of day	min spent	Kcal	
resting	14.9	0.3	432	556.1	
other	29.4	0.2	288	731.6	
foraging	20	0.5	720	1244.2	
				2531.9	**total**

28kg Male

Behavior	MR mlO_2 $min^{-1}kg^{-1}$	proportion of day	min spent	Kcal	
resting	14.9	0.6	864	1730.2	
other	29.4	0.1	144	569.0	
foraging	20	0.3	432	1244.2	
				3543.4	**Total**

Traveling Male

Behavior	MR mlO_2 $min^{-1}kg^{-1}$	proportion of day	min spent	Kcal	
resting	14.9	0.2	288	576.7	
grooming	29.4	0.2	288	1138.0	
foraging	20	0.2	288	774.1	
surf swim[1]	29.61	0.2	288	1146.1	
sub swim[1]	17.55	0.2	288	679.3	
				4314.3	**Total**

Many important questions remain about the energetic and thermoregulatory challenges facing sea otters, and we hope that the methodological approach we have used here will also prove fruitful for future studies. One such question is raised by the considerable range of behavioral strategies found within sea otter populations. Because feeding strategies and foraging effort differ between individuals and also change with population status (Chapter 5 this report, Estes et al. 2003), it is important to understand how this variation impacts energetic costs. For example, could differences in the diving costs associated with different prey specializations (Chapter 6, this report) mitigate the apparent discrepancies in the net energetic benefits of different strategies (Chapter 5)? Further experimental measurements of the costs associated with different diving patterns will hopefully allow us to address this question.

Also of interest from a thermoregulatory perspective are juveniles and lactating females. Juveniles may face elevated energetic challenges simply because of their small body size (low surface area to volume ratio), and so their behavior may be even more constrained by

thermoregulatory requirements for this age class. Lactation is considered to be energetically expensive for all female mammals (Hammond and Diamond 1997), and this may be particularly true for a small mammal in a marine environment. Anecdotal observations on females with small pups show that they spend a few days post parturition at the surface tending to the pup and forgo foraging almost entirely. This decreased activity and lack of supplemental heat produced by HIF may have large impacts on thermoregulation during these times. How a female tending to a small pup is able to maintain body temperature during inactive periods is unclear and will require further study.

Chapter 8. The energetics of foraging in large mammals: A comparison of sea otters with marine and terrestrial predators

Terrie M. Williams and Laura Yeates

Abstract

1. The combination of large body size, carnivory and endothermic costs leads to high caloric demands in mammalian predators. Tactics used to capture prey to meet these demands vary among marine and terrestrial mammals, and ranges from prolonged tracking to high-speed chases. For sea otters, abundant small prey or a single large prey item may be taken on individual foraging dives.
2. To determine the behavioral and energetic consequences of these different foraging methods and habitats, we measured the energetic cost of hunting, energy acquired from ingested prey, and patterns of energy acquisition in free-ranging sea otters (mass = 25 kg). The values were then compared to Weddell seals (body mass = 461 kg) and to terrestrial predators ranging in mass from 25 kg to 170 kg.
3. We found that foraging dive duration was 2.4 $\pm$ 0.4 min for otters specializing on turban snails and 16. 3 $\pm$ 0.6 min for seals; foraging dives were interspersed with short to moderate duration rest periods. In contrast, large terrestrial mammals hunted in 1-2 sessions per day that lasted several hours.
4. The efficiency of an individual hunting event ranged from 3.8 in the sea otter to 10.2 for Weddell seals. This compared to 2.2 for African wild dogs and 3.8 for African lions feeding on ungulates.
5. In general, adaptations for marine living including elevated basal metabolic rates and the dive response represent major influences on hunting efficiency in marine mammals including sea otters. This is further modified by the energetic cost of specific hunting tactics.

Introduction

Survival by large carnivorous mammals requires a continuous balance between energy expended in daily living and energy acquired by hunting (Stephens and Krebs, 1986). To accomplish the latter, mammalian predators display a wide range of techniques for locating, capturing and killing prey. In the terrestrial environment, hunting behaviours range from the cautious stalk and ambush of leopards (Estes, 1991) to the high-speed chases of cheetahs (Caro, 1994). Among the large canids and felids, hunting can be a coordinated group activity as exemplified by African wild dogs and African lions (Schaller, 1972; Packer *et al*., 1990) or solitary forays as typically displayed by cheetahs (Caro, 1994), leopards (Schaller, 1972) and many species of foxes (Estes, 1991). Depending on the size of the predator and hunting style, numerous small prey or single large prey items may be taken to satisfy daily energy needs.

Although large terrestrial and marine predators display many similar hunting tactics, the constraints on acquiring prey differ markedly. Sensory modalities used to detect prey, and thermal and locomotor costs differ due to the unique physical characteristics of air and water (Dejours, 1987). Perhaps, the most obvious difference between these two hunting environments is the accessibility to air. Unlike terrestrial mammals, aquatic mammals must shuttle between two important resources when hunting, oxygen in air above the water surface and the prey located at depth. The result is a marked effect on foraging behaviour and economics (Dunstone and O'Connor, 1979a,b; Kramer, 1988).
In view of the diverse methods of hunting and the constraints imposed by different habitats, we would expect that energetic costs and benefits associated with foraging differ for marine and terrestrial carnivores. Furthermore, sea otters may demonstrate overall higher daily hunting costs due to their relatively high metabolic demands (Williams, 1989). To address this, we determined the cost of hunting for two species of marine mammal, the sea otter (*Enhydra lutris*) and the Weddell seal (*Leptonychotes weddellii*) representing small and large species with different foraging styles. Energetic cost of hunting dives, energy acquired from ingested prey, and patterns of energy acquisition determined from daily activity budgets were assessed. Results for the marine mammals were compared to published values for terrestrial mammals including the African wild dog (*Lycaon pictus*) and African lion (*Panthera leo*). We found that the cost of hunting differed between the two marine mammals as well as between marine and terrestrial carnivores. Moreover, daily energetic balance depended on whether the mammal hunted on land or in water.

Methods

Study Animals

One adult female sea otter (estimated body mass = 25.0 kg) and four adult female Weddell seals (body mass = 461.3 $\pm$ 36.1 kg) and were used in the behavioral field studies. The sea otter in the present investigation was one of 45 study animals captured with diver-held Wilson traps along the coast of San Simeon, California during October 2001-2003. All otters were surgically implanted with a calibrated temperature-sensitive VHF radio transmitter (Advanced Telemetry Systems, Isanti, MN) and provided with a color-coded

flipper tag according to Tinker (2004). Following instrumentation the otters were immediately released at the point of capture. Behavior of free-ranging sea otters was monitored over a two year period following instrumentation. The seals were captured with a purse-string net on the sea ice near Ross Island (McMurdo Sound, Antarctica) in November and December of 2002 as part of an NSF Polar Programs study. After a 24 – 48 h holding period the animals were instrumented with a video-data recording system and swimming stroke monitor as described in Davis *et al.* (1999) and Williams *et al.* (2004). Following instrumentation, the animals were released into a diving hole in the ice and were free to forage, move throughout the Sound, and dive to the ocean bottom at approximately 585 m in depth. After 4 to 8 days, the instruments were removed for data and video retrieval.

In addition to the behavioral studies, the energetic cost of diving was determined for two captive, adult male sea otters (body mass = 26.0 $\pm$ 1.0 kg) diving in a 9.1 m deep water tower and for nine wild, adult Weddell seals (1 female, 8 males; body mass = 387.4 $\pm$ 6.6 kg) diving from an isolated hole in McMurdo Sound (Kooyman *et al*., 1977). The sea otters were maintained in outdoor fiberglass holding pools (4.2 m diameter, 1.2 m deep; 6.0 m diameter, 1.5 m deep) at the California Department of Fish and Game (Santa Cruz, CA) and fed a mixed invertebrate diet. Fresh seawater was continuously added to the pools at ambient ocean temperatures. On test days, the otters were moved to the diving tower for approximately one hour metabolic trials.

Oxygen Consumption during Diving

The energetic cost of diving was determined from the difference between resting and recovery oxygen consumption of sea otters and Weddell seals immediately following individual dives. Details of the open flow respirometry system, experimental protocol, and analysis for Weddell seals have been presented in Williams *et al.* (2004). An identical respirometry system was used for sea otters trained to dive in a seawater storage tower (6.0 m diameter, 9.1 m deep, UCSC). Measurements were made on post-absorptive animals as confirmed by video recordings (Weddell seals) or by a 12 hour overnight fast (trained sea otters). Breathing by all diving animals was limited to a Plexiglas dome mounted at water level over the isolated ice hole or water tower. Subsamples of the dome exhaust were dried (Drierite, Hammond Drierite Co., OH) and scrubbed of carbon dioxide (Sodasorb, Chemetron, MO) before entering an oxygen analyzer (model FC1-B, Sable Systems, Henderson, NV). Air was pulled through the domes at 80-510 $l.min^{-1}$ using a vacuum pump (Sears Wet/Dry Vac, Chicago, IL) or mass flow meter (Sable Systems, Henderson, NV). Oxygen content of the samples was logged every 0.5-1.0 sec on a laptop computer and the rate of oxygen consumption calculated using the equations of Davis *et al.* (1985). All values were corrected to STPD and each system was calibrated daily with nitrogen and standard gases according to Fedak *et al*. (1981).

Hunting Behaviour and Activity Budgets

Daily activity pattern and prey consumption of wild sea otters were determined by 24 hour observation sessions using a 30 x spotting scope (Questar Inc., Isanti, MN) following the methods of Ralls and Siniff (1990). Surface and submerged activities were determined from changes in the character of the transmitted radio signals (i.e. interrupted signals represented

diving bouts), making it possible to measure activity patterns and time budgets during the hours of darkness. Parameters recorded included behavior (rest, grooming, swimming, diving and feeding), duration of surface and submerged intervals, and size and identification of prey species ingested. These data were correlated to time, location, and weather conditions. Prey identification during daylight hours was facilitated by the surface feeding behavior of sea otters and their coastal location. For this study we assumed that prey specialists did not change the type of prey consumed during the night, and estimated nocturnal prey ingestion according to Ralls *et al.* (1995).

Underwater behaviors of the Weddell seals were monitored continuously using a video-data logging system carried by the animal as it dove below the sea ice. Details of the instrumentation, attachment procedures, and analyses have been described previously (Davis *et al*., 1999; Fuiman *et al*., 2002; Williams *et al*., 2004). A low light-sensitive camera with an array of near-infrared LEDs was mounted on a neoprene patch that was glued on the fur of the head. The camera provided a view of the seal's eyes and muzzle, and of the water for approximately 70 cm in front of the nose. Video images were recorded and synchronized in real time with dive depth that was monitored with a pressure transducer. All videos were screened for encounters with prey. Mouth movements were not in the field of view; therefore, we used visual detection of prey within 10 cm of the Weddell seal's muzzle and coincident head movements to denote fish ingestion. Daily activity budgets of the Weddell seals were reconstructed from the video recordings and divided into dive and rest periods. Because the animals rested submerged, on the water surface and lying on the ice, rest periods included all quiescent times when the seals were hauled out or at < 50m in depth. Only dives in which seals fed exclusively on Antarctic silverfish (*Pleuragramma antarcticum*) were analyzed in this study.

Hunting Efficiency

The efficiency of hunting was defined as the ratio of energy acquired from the ingestion of prey to the energy expended during a single hunting event. Hunting events for marine mammals were delimited by individual dives in which prey were encountered (seals) or brought to the water surface (otters). For Weddell seals, the energy acquired was determined from the average number of fish ingested on a foraging dive and an average caloric content of 78 kcal (325 kJ) per fish (Castellini *et al*., 1992). The energy expended for hunting was calculated from the average duration of individual foraging dives and the relationship between oxygen consumption and dive duration (eq. 3 in Williams *et al*., 2004). Similarly, the energy acquired by sea otters eating turban snails (*Tegula* spp.) was calculated from the average number of snails obtained on an individual dive with a caloric value of 2 kcal (8.3 kJ) per gm snail (Farout *et al*., 1986). The energy expended for hunting was calculated as for seals using the average duration of foraging dives and the rate of oxygen consumption measured for the same dive duration in the water tower.

Comparative values for hunting efficiency by African hunting dogs and African lions were calculated from published values for daily prey ingestion rates and energetic costs of hunting. These species were chosen due to their body size, carnivorous diet, and availability of data. Ingested energy from prey was calculated from the average mass and caloric content of prey consumed during individual hunting events. On average, food intake by wild dogs is

approximately 3.5 kg meat per day (Gorman *et al*., 1998) generally made in two separate kills (Schaller, 1972). We assumed that 75% of the intake was lean meat at 193 kcal.100 gm^{-1} (808 kJ.100 gm^{-1}) and 25% was viscera at 130 kcal.100 gm^{-1} (544 kJ.100 gm^{-1}) (Geigy, 1981). The energetic cost of hunting for wild dogs taken from Gorman *et al*. (1998) was divided into two hunting periods per day. For lions, we used an average gorging of 7 - 11 kg of meat and viscera from a single kill in the evening (Schaller, 1972) with the same caloric values as above. Energetic cost of the hunt by lions was calculated from activity budgets of nomadic males from Schaller (1972) assuming that resting periods constituted basal metabolic rate (BMR) levels. BMR was determined from the regression for vertebrate eaters from McNab (1988) using an average body mass of 170 kg. The difference between daily field metabolic rate (10,549 $kcal.day^{-1}$ or 511 W; Williams, unpublished data) and energy utilized for resting periods (5485 $kcal.day^{-1}$ or 266 W) represents the energy available for walking, killing and feeding. Because actual hunting periods for lions are difficult to define (Schaller, 1972) we used the entire difference to represent the cost of hunting; that is, when the lions were not resting they were conducting activities associated with hunting. All values for hunting efficiency represent total energy utilization and acquisition, and do not include corrections for assimilation efficiency.

Results

Hunting Behavior and Activity Budgets

Despite differences in predatory tactics, the pattern of hunting and prey acquisition showed many similarities for sea otters and Weddell seals (Fig. 69, Table 20). For both marine mammals, foraging dives were interspersed with short to intermediate duration rest periods on the water surface. For example, one free-ranging seal foraging in McMurdo Sound during the austral summer made 25 dives during a 24 hour period of which 24 involved encounters with Antarctic silverfish. Total time for deep (> 50 m) foraging dives was 471 min. This compares with 969 min spent in shallow water or resting on the surface in periods ranging from approximately 20 min to two longer periods exceeding nine hours each (Figure 69). Overall, the seal spent 41.1% feeding and the remainder of the time resting or at shallow depths.

Table 20. Hunting efficiency of marine and terrestrial carnivores. For marine mammals a hunting event is defined as a single dive. A hunting event by terrestrial mammals is defined by the period to bring down a single prey item. Values are shown as mean ± 1 S.E. N = 37 dives for four Weddell seals feeding on Antarctic silverfish and n = 302 dives for one sea otter specializing on turban snails. Values for African wild dogs were derived from Gorman *et al.* (1998) and for African lions from Schaller (1972) as described in the text.

	Hunt Duration (min)	Hunt Cost ($mlO_2.kg^{-1}$)	Kcal expended	Kcal Ingested	Efficiency
Marine					
Sea otter (25 kg)	2.4 ± 0.4	45.4	5	19	3.8
Weddell seal (461 kg)	16.3 ± 0.6	69.2 ± 3.1	137 ± 7	1,397 ± 77	10.2 ± 0.7
Terrestrial					
Wild Dog (25 kg)	104	----	1,288	2,836	2.2
African Lion (170 kg)	180	----	5,062	19,498	3.8

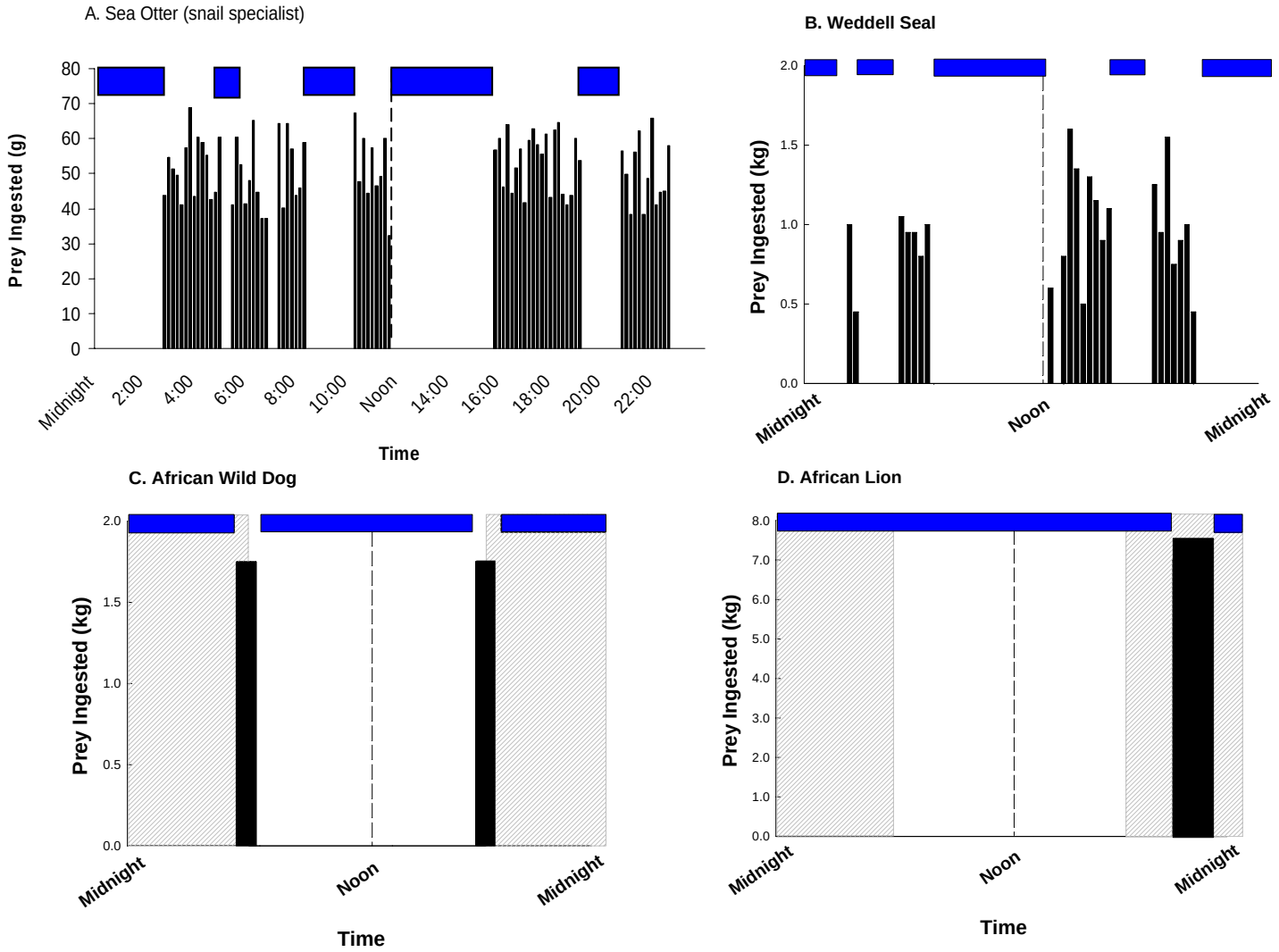

Figure 69. Feeding patterns for large marine and terrestrial mammals. Daily activity pattern and prey ingestion during a hunting day are compared for a sea otter feeding on turban snails (A), an adult Weddell seal feeding on Antarctic silverfish (B), and an adult African wild dog (C) and a nomadic African lion feeding on ungulates (D). Vertical bars represent the timing and mass of prey consumed for individual dives by the sea otter and seal, and timing and mass of meat eaten in a single day by the wild dog and lion. Rest periods are denoted by the horizontal, filled bars at the top of each figure. Values for the sea otter and seal are from the present study. Values for the wild dog are from Gorman *et al.* (1998) and for the lion from Schaller (1972). Periods of darkness for the terrestrial mammals are shown by the shaded areas. Note that during the austral summer in McMurdo Sound there is constant sunlight for the diving seals.

Similarly, sea otters interspersed foraging bouts with resting and grooming periods of 20 to 310 min. Because sea otters showed considerable individual preferences for specific prey, we will focus the remainder of the discussion on one specialist feeding on turban snails, a common prey item for this species (Tinker, 2004). This otter preformed nearly continuous 2.4 min dives (Table 20) during 60 - 200 min foraging bouts that occurred day and night, only taking the time to consume the prey between dives. Overall, the otter spent 50.4% of the day diving for snails, 31.5% resting on the water surface, and 18.1% in other activities including grooming and surface swimming.

Hunting Efficiency

For the sea otter specializing in turban snails, average dive duration was 2.4 $\pm$ 0.4 min SE (n = 302 dives) during which time the animals collected an estimated 5 snails (3 gm each) per dive. Average duration during foraging dives in which the seals consumed *Pleuragramma antarcticum* was 16.3 min $\pm$ 0.6 SE (n = 37 dives). During these dives the seals ingested an average of 18.0 $\pm$ 1.0 SE fish per dive. Using these numbers we calculated the ratio of energy acquired to energy expended during individual foraging events, termed hunting efficiency. Values for hunting efficiency ranged from 3.8 in the sea otter to 10.2 for Weddell seals (Table 20). This compared to 2.2 for African wild dogs of similar body mass to sea otters, and 3.8 for African lions feeding on the meat and viscera of ungulates.

Discussion

A major difference in foraging behavior between marine and terrestrial carnivores is the duration of individual hunting or predation events (Fig. 69). Due to constraints associated with access to air during predation, marine mammals must acquire prey in relatively short forays (Dunstone and O'Connor, 1979a,b; Kramer, 1988). Thus, the duration of individual foraging dives was only 2.4 – 16.3 min in sea otters and Weddell seals. This compares with hunting events that often last several hours in large terrestrial carnivores depending on the size of the prey taken (Schaller, 1972). Such an intermittent style of energy acquisition, while disruptive to rest periods, did not necessarily result in low hunting efficiencies for marine mammals. Rather, the energy expended relative to the energy gained per hunting event was equal to or greater in marine mammals than in the terrestrial mammals examined here (Table 20).

The highest hunting efficiency for an individual predation event was observed for Weddell seals and exceeded those of sea otters, wild dogs, and lions by nearly 3 fold. This could be attributed to the exceptionally low energetic cost of individual dives by the seals, which were associated with metabolic responses occurring with prolonged submergence (Kooyman, 1989). This level of metabolic suppression with submergence was not observed for the sea otters. Because hunting efficiency depends on the time scale examined, differences between terrestrial and marine carnivores was altered and become less distinct when examined for a 24 hour period. For example, the 391 kg Weddell seal in Figure 69 performed 24 foraging dives resulting in a daily energy expenditure for hunting of 3,295 kcal (13,807 kJ). The resulting daily hunting efficiency of 5.1 for Weddell seals was only 34% higher than for African lions.

These results only apply to hunting days, which differs in the pattern of occurrence for the species examined. Sea otters (Ralls and Siniff, 1990), African wild dogs (Gorman *et al*., 1998), and lions (Schaller, 1972) generally hunt daily or within a few days after feeding. These three species generally take in sufficient calories to in a single hunting day to meet the metabolic needs of the animal for 1 –3 days. Thus, the snail hunting sea otter in this study obtained 5,647 kcal (23,663 kJ) in 302 dives to support a daily field energy requirement (based on time energy budgets) of 4,887 kcal (20,478 kJ). Observations showed that this animal fed daily. In comparison, the terrestrial species take in enough food to support the animals for several days. The unusual species in this regard was the Weddell seal. With the energetic cost of a foraging dive averaging 137 kcal (575 kJ, Table 20) and each fish representing 78 kcal (325 kJ), an adult Weddell seal would need to consume 2 fish to remain in caloric balance (Castellini *et al.* 1992). However, once in an aggregation of silverfish, Weddell seals will consume 18 – 20 fish (approx. 900 – 1000 gm) before terminating a foraging dive, and then continue to ingest fish at this rate on several subsequent dives (Fig. 69). On any individual foraging dive Weddell seals will consume 11 times the calories required to account for the cost of hunting, or 2 times its daily caloric demands.

Based on these results, we find that a marine lifestyle represents a major influence on hunting behavior and efficiency in large mammals. For both marine and terrestrial species hunting efficiency and the resultant daily caloric balance is further modified by the energetic cost of specific hunting tactics. The cost of locating prey, the predictability and abundance of prey, and the number of successful and unsuccessful capture attempts will impact hunting efficiency, especially as marine and terrestrial habitats are altered. In view of this, further investigation concerning the relationship between energy resources provided by the environment and the physiological capabilities and limitations of energy acquisition in large predators including sea otters is warranted.

Chapter 9. Summary of Health Parameters in Radio-tagged Southern Sea Otters

Dave Jessup, Michael J. Murray, Melissa Miller, Erin Dodd

Abstract

1. During the years 2001 and 2002 seventy two southern sea otters which were captured for marking and released for subsequent field study were also blood sampled to help establish their state of health, exposure to infectious diseases and other factors.
2. In general the sea otters captured were in good condition, showed little evidence of chronic health problems, although some had extensive tooth wear.
3. Blood chemistry and hematology values were generally within normal ranges for wild sea otters but some had evidence of acute stress associated with capture. Some measures of immune system function were utilized and again, significant abnormal findings were not noted.
4. The otters were also tested for evidence of exposure to selected diseases, those which are potentially important and for which antigen or antibody based tests have been developed.
5. The integration of ecological and biological data with health assessments will allow further investigation of risk factors that may be important in determining morbidity and mortality in this population.

Introduction

Southern sea otters were listed as "threatened" under the ESA in 1977. A number of lines of evidence suggest that these populations suffer from relatively high adult mortality and a low growth rate (Estes et al 2003). Diseases and parasites appear to account for approximately 40% of overall mortality based on examination of fresh dead sea otter carcasses (Thomas and Cole, 1996). Many of the diseases that have been identified by pathologists have a relatively long time course and may be apparent on physical examination by analysis of blood tests that can help determine function of various organ systems, immune system function, and general health. Blood samples were taken subsequent to induction of anesthesia and processed within 4-8 hours by standardized materials and methods in commercial laboratories or selected university research laboratories. Serum derived from whole blood was also examined for antibodies that show that exposure to certain viral, protozoal or bacterial pathogens have occurred during the animal's life. This work helps establish baseline health and disease exposure rates for the population of living animals.

Methods

All animals were captured by use of Wilson traps guided by divers (Benz and Britton, 1995). A period of time from 30 minutes to an hour or so elapsed before the animal could be brought to the shore, but during this interval otters are kept wet and cool. They were either transported in modified kennels or transferred to kennels when they arrive at a dock and then rolled to waiting mobile veterinary surgical facilities. They were weighed and anesthesia induced with fentanyl and diazepam (Monson *et al.* 2001). They were usually measured, marked and sampled just before or just after surgery (approximately 1-1 1/2 hours post capture). Anesthesia was maintained with an isoflourane gas and oxygen mixture.
An initial examination was done on all animals including auscultation of heart and lungs, examination of mucus membranes for oxygenation and palpation of the abdomen. Oxygen saturation of blood was regularly monitored by pulse oximetry as was rectal temperature. Various weights and measures were taken as well as observations of old wounds, fractures or other injuries, tooth wear and other physical abnormalities. Up to 60 cc of blood was collected, from the jugular vein in most cases, for the various tests reported here, for other research and for banking. Colored plastic tags were attached into the webbing of the hind toes and a passive integrated transponder (PIT) chip inserted under the skin of the groin.

Radiographic images were taken in some cases to locate the telemetry instruments in the abdomen or to confirm pregnancy that could not be confirmed by palpation (pregnant animals were not implanted). After aseptic preparation and sterile draping an approximately 8 cm ventral midline incision was made centered between the umibilicus and the prepucial opening (males) or the cranial aspect of the mammary glands (females). In the vast majority of animals the abdomen appeared healthy and a VHF transmitter and time depth recorder were inserted into the abdominal cavity. Closure of the surgical incision was done in four layers with polydioxanone suture material (PDS II ™, Ethicon, Inc, Somerville, New Jersey). When all procedures were completed gas anesthesia was turned off and animals were moved to iced kennels and the narcotic antagonist naltrexone was given. Most animals were alert

and active within two to four minutes and were subsequently transported to waiting boats for release close to the capture site or released from shore.

Results

As noted most otters examined were in good body condition. Of the animals subject of this report capture records indicate noted health concerns based on physical examination in only two. Severe tooth wear was noted in 12 individual animals.

Results of serum chemistry panels are shown in Table 21 for all animals and years. Of note, CPK and AST levels are similar to those seen in other wild sea otters (Jessup, unpublished) but above those expected for healthy rested otters not subjected to physical exercise or stress (Dierauf and Gulland, 2001). Elevations of this nature are usually due to exercise and some muscle lysis resulting from struggling and physical restraint or may be an artifact associated with hemolysis of the collected blood sample and do not seriously compromise most animals. Blood glucose levels were also somewhat variable with a few individual animals that might be considered hypoglycemic or hyperglycemic as compared with levels reported by Deirauf and Gulland 2001. In our experience this is also often the result of moderate stresses of capture and handling and usually self correcting.

Results of complete blood counts for both locations and years are summarized in Table 22. As compared with cats and dogs, sea otters have relatively high hematocrit (HCT), hemoglobin (HGB) and blood urea nitrogen (BUN), characteristics which are believed to be adaptations to diving and a high protein diet (Williams and Pulley, 1983). White blood cell counts we report here show more variability than reported Dierauf and Gulland 2001. IgG levels were determined by a quantitative assay developed specifically for sea otters and do not suggest inadequate immunoglobulin levels (a measure of humoral immune response) in the animals tested.

Table 21. Summary of Mean, Standard Deviation, Minimum Value, and Maximum Value for sea otter serum chemistry results.

SERUM CHEMISTRY	Count	Mean	Standard Deviation	Minimum	Maximum
ALKP IU/L	72	112	32	47	232
ALT IU/L	72	197	186	92	1368
AST IU/L	72	226	315	99	2779
CPK IU/L	72	1051	1824	208	14466
GGT IU/L	72	14	4	0	22
AMYLASE	43	6	11	0	60
LIPASE	43	33	46	0	318
ALB g/dL	72	2.5	0.2	2	3
TP g/dL	72	6.4	0.9	0.1	7.7
GLOB g/dL	72	3.9	0.5	2.9	5.3
T BILI mg/dL	72	0.1	0.1	0	0.5
DIR BILI mg/dL	72	0.0	0.0	0	0.2
BUN mg/dL	72	65	13	40	94
CREAT mg/dL	72	0.6	0.1	0.4	1
CHOL mg/dL	71	188	84	116	783
GLU mg/dL	72	130	36	75	228
CA mg/dL	72	10.6	12.0	7.2	81
PHOS mg/dL	72	5.4	1.5	2.8	8.9
BICARB mEq/dL	72	25	5	14	35
CL mEq/dL	72	116	4	105	125
K mEq/dL	72	4.3	0.4	3.3	5.7
NA mEq/dL	72	154	3	142	162
A/G ratio	72	0.7	0.1	0.4	1
B/C ratio	57	68.6	45.4	0	158
INDIR BILI mg/dL	72	0.1	0.1	0	0.3
NA/K ratio	72	36	3	25	46
ANION GAP mEq/L	72	18	6	5	32
T4 ug/dl	71	2.0	1.1	0.6	6.8

Table 22. Summary of Mean, Standard Deviation, Minimum Value, and Maximum Value for sea otter complete blood count (CBC) results.

COMPLETE BLOOD COUNT	Count	Mean	Standard Deviation	Minimum	Maximum
WBC 10^3/uL	71	7.0	2.7	2.3	17.5
RBC 10^6/uL	70	4.93	0.53	3.09	5.94
HGB g/dL	71	18.4	2.0	11.3	22.4
HCT %	71	52.2	5.9	31.2	62.4
MCV fL	71	104	15	1.4	120
MCH pg	71	37.5	1.7	33.2	42.3
MCHC g/dL	71	35.5	1.8	33	44.3
NRBC %	41	0.10	0.44	0	2
BANDS %	42	0.64	4.17	0	27
NEUT %	71	59.36	14.65	14	85
LYMPH %	71	31.41	13.20	0	65
MONO %	71	4.62	3.19	1	15
EOS %	65	3.85	6.47	0	35
BASO %	58	0.14	0.35	0	1
BANDS #/uL	41	89	573	0	3666
NEUT #/uL	71	4080	2386	63	14700
LYMPH #/uL	71	2054	1095	0	5270
MONO #/uL	71	308	234	3	875
EOS #/uL	66	281	525	0	2970
BASO #/uL	58	7	21	0	78
Average Of IgG (mg/ml)	72	18.07	6.33	6.58752	34.56192

Results of immunoflouescent test for antibodies to *Toxoplasma gondii* are shown in Table 23 and to *Sarcocystis neurona* in Table 24. In general titers less than 1:320 are considered negative and greater 1:320 are considered positive. Despite samples size and sex biases it is clear that a significantly higher proportion of animals sampled in the Piedras Blancas area have been exposed and likely infected with *T. gondii*. Interestingly, this pattern does not hold for *S. neurona.*

Table 23. Summary of sea otter *Taxoplasma gondii* titers.

CAPTURE LOCATION / YEAR	*T. gondii* Titer <320	*T. gondii* Titer >320
Point Conception 2001 n=14	7	7
Point Conception 2002 n=10	8	2
Piedras Blancas 2001 n=15	7	8
Piedras Blancas 2002 n=31	9	22

Table 24. Summary of sea otter *Sarcocystis neurona* titers.

CAPTURE LOCATION / YEAR	*S. neurona* Titer <320	*S. neurona* Titer >320
Point Conception 2001 n=14	10	4
Point Conception 2002 n=10	9	1
Piedras Blancas 2001 n=15	13	2
Piedras Blancas 2002 n=31	23	8

Table 25 shows results of tests for antibodies to four morbiliviruses (canine distemper (CDV), phocine distemper (PDV), phocine morbilivirus (PMV) and dolphin morbilivirus (DMV)) and a canine parvovirus. All were negative. Table 25 also shows results of tests for antibodies to seven strains of Leptospirosis, *Brucella abortus* (thought to cross react with marine *Brucella spp*.) and *Chlamydophila*. Antibodies to *Brucella* were detected in three adult males from Pt. Conception.

Table 25. Summary of serologic results for sea otters tested from Pierdras Blancas and Point Conception areas in 2001 and 2002. Three adult males from Point Conception in 2001 had positive titers to *Brucella abortus* and three adult males from Pierdras Blancas in 2002 had anti-compliment results to the Chlamydia serologic test.

DIAGNOSTIC LABORATORY	SEROLOGIC TEST	# of Sea Otters Tested	# of Positives
Oklahoma Animal Disease Diagnostic Lab	CDV	58	0
Oklahoma Animal Disease Diagnostic Lab	PDV	58	0
Oklahoma Animal Disease Diagnostic Lab	PMV	58	0
Oklahoma Animal Disease Diagnostic Lab	DMV	58	0
Washington Animal Disease Diagnostic Lab	Canine Parvovirus	61	0
Washington Animal Disease Diagnostic Lab	*Brucella abortus*	61	3
Washington Animal Disease Diagnostic Lab	*Leptospira autumnalis*	6	0
Washington Animal Disease Diagnostic Lab	*Leptospira bratislava*	61	0
Washington Animal Disease Diagnostic Lab	*Leptospira canicola*	61	0
Washington Animal Disease Diagnostic Lab	*Leptospira grippotyphosa*	61	0
Washington Animal Disease Diagnostic Lab	*Leptospira hardjo*	61	0
Washington Animal Disease Diagnostic Lab	*Leptospira icterhaemorrhagiae*	61	0
Washington Animal Disease Diagnostic Lab	*Leptospira pomona*	61	0
National Veterinary Services Lab USDA	*Chlamydia*	9	3 anti-complimentary

Discussion

Most animals examined during the course of this study appeared to be in good health. Serum chemistry and blood count data supports this generalization, although much variation was evident in these wild-caught otters. Complete blood counts with quantitative IgG allow determination of some simple measures of circulatory system, bone marrow, immune system function. More detailed determinations of immune function have been undertaken on other populations of southern sea otters, but due to logistical problems associated with sample handling, shipment and treatment, relatively few animals from these locations could be used in that work and data is not reported here.

Rates of exposure to infectious diseases may vary by area, age, sex or other risk factors. Morbilliviruses are thought to be a significant threat to marine mammal populations (Osterhaus and Vedder, 1988) and sea otters, as mustellids, are believed likely to be very susceptible to all or several of those viruses, although naturally occurring disease has not been reported. Parvoviruses originally from cats, are thought to have adapted to mink, dogs and raccoon resulting in serious disease and high levels of mortality, so they too may pose a threat to sea otters. No evidence of morbilivirus or parvovirus exposure was detected.

A high proportion of otters living in the Piedras Blancas were seropositive to *Toxoplasma gondii*, which may suggest that otters living in that area are at higher risk of exposure to this recogniozed sea otter pathogen. From 1998 to 2001, *T. gondii* was the primary cause of death for over 16 % of freshly dead, necropsied otters (Kreuder et al 2003). The ecology of *T. gondii* infection of sea otters and the route and means of land to sea transfer of this protozoan, which is only known to complete its life cycle in cats, is still under study. But areas of the California coast where there are significant freshwater inputs, and Morro Bay in

particular (Miller et al 2002), are areas where risk of infection is significantly higher than other portions of the California coast. *S. neurona* is a similar parasite to *T. gondii* but it completes its life cycle in the opossum (*Didelphis viginianus*), another introduced and invasive species. In April of 2004 a sea otter die off caused primarily by *S. neurona* (Miller et al, unpublished) centered around Morro Bay killed approximately 30 sea otters. Since a relatively high proportion of southern sea otters die from infectious diseases, trying to determine the risk factors for the living population is important.

Analyses of blood samples taken from otters in this study for persistent organic pollutants are awaiting funding. Genetic analysis for determination of genetic diversity, kinship patterns, effective population size and diversity at the major histocompatability complex (MHC), sites that are most closely associated with resistance to bacterial and protozoal infection, have recently been completed but data is not available for inclusion in this report. Integration of genetic and pathology data are underway.

The opportunity to sample and examine sea otters captured for ecological research offers the opportunity to assess and measure the health of living animals in the population. This approach offers a different picture of health than examination of dead sea otters (just as examination of rather randomly selected people from a healthy population would provide different information than examining dead people that arrive at the morgue). The health assessment portion of this work allows quantitative evaluation of health of sea otters from two locations at the time of capture. Recaptures allow a second or even occasionally a third opportunity to follow the health of individual animals, many of which are also intensively monitored by shore observers. By integrating ecological, food habits, movement, body temperature and other information with health and disease data we can get a much more complete picture of what factors may influence morbidity and mortality.

Chapter 10. Causes of Mortality in Radio-tagged Southern Sea Otters

Melissa A. Miller, Dave Jessup, Erin Dodd

Abstract

1. Of 72 southern sea otters captured for sampling, marking and field observation between 2001 and 2002, 17 otters were confirmed dead and their carcasses were submitted to CDFG for necropsy by a veterinary pathologist. For 1 additional otter, the VHF transmitter was recovered from a tide pool, but no carcass could be located for postmortem examination.
2. For all recovered carcasses, necropsy was performed at the California Department of Fish and Game (CDFG) at Santa Cruz, California by a veterinary pathologist. Primary and contributing causes of death as well as pertinent biological findings were recorded for all necropsied sea otters.
3. Where appropriate, additional diagnostic tests such as bacterial culture, serological testing, parasite isolation in cell culture and testing for the marine biotoxin domoic acid were completed.
4. Patterns of mortality with respect to gender, age class, nutritional condition, location and other factors were examined.
5. Combining mortality data with life history data for the same animals over time will provide critical insight into the complete life history of this federally listed threatened species. Our findings should help to determining if the patterns of mortality observed in tagged otters are comparable with mortality trends observed in the general population.

Introduction

Southern sea otters (*Enhydra lutris nereis*) have made a slower than expected recovery after commercial fur harvest drastically reduced their numbers prior to the 20th century (Riedman and Estes, 1990). Sea otters serve as excellent biological indicator of the health of a marine ecosystem heavily influenced by human activity because they live close to shore, generally remain in one geographically localized area for most of their lives and consume large amounts of benthic and midlevel invertebrates. Numerous studies have revealed that these prey are highly efficient bioaccumulators of bacteria, viruses, parasites and anthropogenic contaminants (Nakata et al., 1998; Kanaan et al., 1998; Lindsay et al., 2001; Arkush et al., 2003). Thus, patterns of mortality in sea otters may provide critical insight into the broad-reaching effects of anthropogenic change to coastal systems.

There is little disagreement among experts that high mortality, not decreased reproduction appears to be the major factor limiting southern sea otter recovery (see Chapter 2, this report, Estes *et al.* 2003, Thomas et al., 1996: Kreuder et al., 2003). Studies have detected elevated tissue burdens of contaminants in southern sea otters with infectious disease (Nakata et al., 1998; Kanaan et al., 1998), as well as an usually high proportion of mortality due to infectious disease in stranded otters (Thomas et al., 1996; Kreuder et al., 2003). Two retrospective analyses of specific causes of southern sea otter mortality using stranded carcasses have been conducted (Thomas et al., 1996; Kreuder et al., 2003). The first study focused on patterns of mortality for carcasses recovered between 1992 and 1995 (Thomas et al, 1996). The second study also relied on carcass recovery and spanned the years 1998 to 2001 (Kreuder et al., 2003). Both studies identified a wide range of causes of mortality. However, in both studies, several key causes of death contributed the most to overall mortality. These included mortality due to infectious agents, such as intestinal thorny-headed worms, or acanthocephalans (*Profilicollis spp*.), protozoan parasites (*Toxoplasma gondii* and *Sarcocystis neurona*) and a wide range of bacteria (Thomas et al., 1996; Miller et al., 2001; Miller et al., 2002a; Mayer et al., 2003; Johnson et al., 2003; Kreuder et al., 2003; Stavely et al., 2003). An additional common cause of death was shark predation (Ames, et al., 1996; Thomas et al., 1996; Kreuder et al., 2003). Overall, both studies identified a disturbingly high proportion of mortality attributed to infectious disease. Interestingly, mortality due to infection by acanthocephalans and protozoa were not recognized as a common cause of mortality in otters prior to 1992, in part due to differences in carcass examination techniques. In addition, spatial patterns of mortality have been described, including high-risk areas for mortality due to acanthocephalan-associated peritonitis (Mayer et al., 2003; Kreuder et. al., 2003), *T. gondii*-associated meningoencephalitis (Kreuder et al., 2003), cardiovascular disease (Kreuder et al., in press) and shark bite (Ames et al., 1996; Kreuder et al., 2003).

It is currently unknown if causes and patterns of mortality in stranded otters mimic those of the free-living sea otter population, since stranded carcass recovery may be biased with respect to cause of death, location, carcass size, wind, currents and other factors. The present study provides the first preliminary data to link detailed life history information from the living animals with data on the specific causes of death, a step which is critical to understanding patterns and impacts of disease in this threatened species. For the first time we were able begin the process of interweaving life history data with findings from detailed postmortem examinations, and to examine patterns of mortality with respect to demographic

factors, prey selection, foraging behavior, reproductive activity and coastal location. In addition, this approach facilitates the future examination of potential anthropogenic impacts due to such factors as surface runoff, municipal sewage outfall and human population density, as the body of data is increased over time. This study provides a unique opportunity to begin to glimpse how specific patterns of mortality may be influenced by behavioral strategies and specific anthropogenic impacts. Over time, this information can help to more efficiently direct management efforts to mitigate negative environmental impacts and facilitate long-term sea otter survival.

Methods

Between 2001 and 2004, 17 southern sea otters that had been tagged during the course of this study and were subsequently recovered as carcasses were examined by CDFG at Santa Cruz, California. Full body radiographs were completed to detect bullets or gun-shot, shark teeth, or other lesions prior to completing the necropsy. Otter age was recorded on the basis of previously established length, body weight, and dentition criteria (Morejohn et al., 1975). A detailed necropsy was performed on each animal. Where appropriate, selected tissues were screened for pathogenic bacteria, fungi, and protozoa. If whole blood was available, serum was separated via centrifugation and stored at -70 C until tested. For all freshly dead otters and for selected otters in moderate to advanced postmortem condition, tissues were immersion-fixed in 10% neutral buffered formalin, trimmed, dehydrated and embedded in paraffin. Five μm sections were cut using a rotary microtome, deparaffinized, stained with hematoxylin and eosin (H&E), and examined using a compound microscope.

For selected otters, samples of cerebrum and cerebellum were collected aseptically into chilled, sterile antibiotic saline solution (0.85% saline with 100 IU/ml penicillin G and 100 μg/ml streptomycin), homogenized and placed over stationary cultures of monkey kidney (MA104) as previously described (Miller et al., 2001; 2002a). Cell cultures were considered positive when characteristic refractile intracytoplasmic protozoal cysts, or motile extracellular zoite stages, or both, were first observed. The identity of each protozoan isolate was confirmed through parasite morphology in cell culture, antigenic characterization or molecular characterization, as previously described (Miller et al. 2001; 2002a). Cell cultures were maintained for at least 1 month after brain tissue inoculation before being deemed negative and discarded. *Protozoal* infection in sea otters was confirmed via isolation and characterization of *T. gondii* in cell culture from brain homogenate, observation of parasites on histopathology, or both. For serum collected antemortem and at the time of necropsy, an immunofluorescent antibody test (IFAT) was performed as previously described (Miller et al., 2002a). Endpoint titers were determined by serial dilution. Wells were examined using fluorescence microscopy and the last well with distinct parasite outline fluorescence was the reported titer.

The primary and contributing causes of death were determined after examination of available clinical, diagnostic, gross and microscopic data for each case. Where greater than one pathological process was detected in the same otter, the primary cause of death was considered to be the most significant and immediate finding that could have resulted in the animal's death. If multiple factors were felt to be inter-related (for example, acanthocephalan

peritonitis leading to bacterial peritonitis and sepsis), the first event leading to the animal's death was listed as the primary cause of death (eg acanthocephalan peritonitis). In cases where two independent, but equally significant causes of death were detected in the same otter (eg acanthocephalan peritonitis and protozoal meningoencephalitis), the cause of death that was felt to be the most immediate cause of morbidity and mortality was selected as the primary cause of death, and the second cause was listed as a contributing cause of death. Selected contributing causes of death are discussed in greater detail in the Results.

Results

Of 72 southern sea otters captured for sampling, radio-tagging and field observation between 2001 and 2004, 17 were confirmed dead and their carcasses were submitted to CDFG for necropsy by a veterinary pathologist. Eight additional otters were lost to further follow-up and are assumed to be dead, while 47 remain alive and were monitored in the field until very recently (see Chapter 1, this report). For one necropsied otter, the necropsy information was not available at the time of compilation of this report. Thus, the data presented here will cover 16 tagged and necropsied sea otters. For one additional otter, the VHF transmitter was recovered from a tide pool, but no carcass was found. This transmitter had been broadcasting a normal living signal (i.e. active, normal temperature range) 5 days prior to detection of a changeover to mortality signal and recovery of transmitter from the tide pool. The cause of death for this animal is unknown.

For the 16 necropsied otters, 6 were recovered in fresh (≤72 h dead) postmortem condition, 5 were moderately decomposed (carcass intact but autolyzed) and 5 were in an advanced state of decomposition (marked autolysis, often with sloughed skin and body parts). At least half of the submitted carcasses had some degree of postmortem scavenging prior to receipt for necropsy, ranging from mild (eyes missing) to extensive (carcass essentially skeletonized). The sample population of 16 otters was composed of 8 males and 8 females. Most of the sample population was composed of aged adult or adult otters: 43.8% were aged adults, with the same percentage of adults (7/16 each), compared to 6.2% each of immature and sub-adult otters (1/16 each) and no pups. This age-structure is not entirely surprising as pups and juveniles were not targeted for capture (sea otter pups could not be safely implanted with intraperitoneal transmitters due to their small size). In terms of nutritional condition at the time of necropsy, 12 of the otters had scant to no subcutaneous fat, compared to 2 with moderate fat and 2 with abundant fat.

Carcass recovery was uneven across the sea otter range: One carcass was recovered from the Monterey Bay region and 15 dead otters were recovered from all other locations in the sea otter range. All but one carcass (93.8%) was recovered from the southern half of the sea otter range and 12/16 of the carcasses (75%) were recovered within 50 km of each other in the vicinity of San Simeon, California. Seasonal carcass recovery trends were as follows: 2 of 16 total carcasses were recovered in the winter months (December-February) 3 were recovered in the Spring (March-May), 6 in the summer months (June-August) and 5 in the fall (September-November). This is relatively consistent with the seasonal pattern observed in the carcass database: the greatest proportion of strandings typically occurs in the spring and summer months.

The primary causes of death for each necropsied otter are shown in Figure 70. The most common primary causes of death were acanthocephalan peritonitis (4), cardiac disease (2), shark bite (2) and intestinal twist or volvulus (one of each condition). One adult female otter had a large nose wound, was emaciated and was lactating. The period of postpartum pup care to weaning appears to be an especially stressful time for adult female sea otters. Pup weaning often coincides with estrus and copulation with territorial males, which in this population is frequently associated with additional physical trauma and stress. Thus, the end lactation period in breeding adult females is a period of special concern for recovery of the southern sea otter. Another adult female otter died due to an unusual form of mating trauma: A male otter had been observed copulating with the female just prior to death. Afterward the female was observed to be "swollen" grossly and exhibited difficulty diving to forage. At necropsy, a severe pneumoabdomen was traced to a full-thickness vaginal perforation near the otter's cervix. Pneumoabdomen resulting from forced copulation and vaginal perforation has also been observed in a harbor seal pup that was forcibly mated by a sea otter (Harris et al., manuscript in prep) and aggressive mating activity of sea otters resulting in mortality has been reported previously (Hatfield et al., 1994). Sea otters possess a proportionally large bacculum, or penis bone typical of all mustelids which may help explain the vaginal trauma that may result from forced copulation.

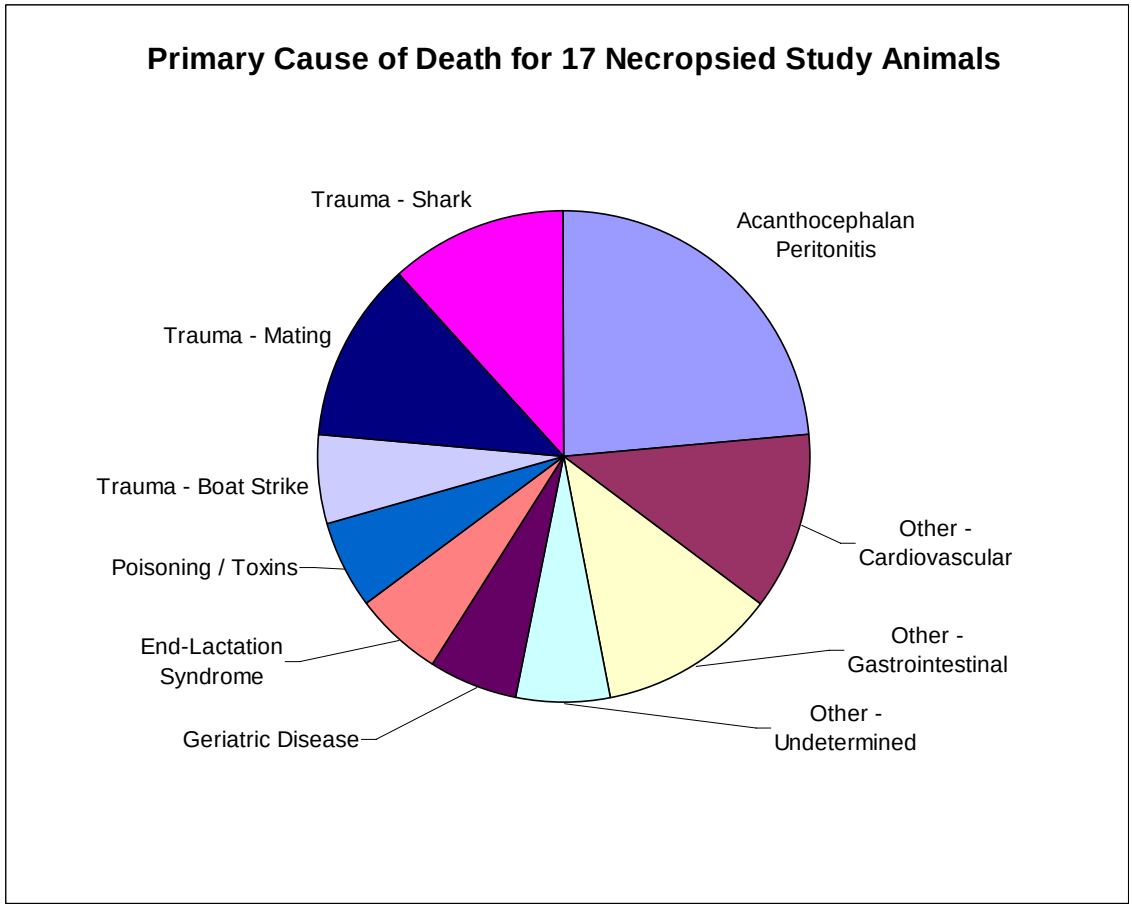

Figure 70. Pie chart depicting primary causes of death for 16 sea otters recovered dead during the course of this study, and one additional otter for which only the VHF transmitter was recovered.

One additional adult female otter died due to uterine torsion and breech presentation of a large, full-term fetus. The fetal membranes were ruptured, indicating that the animal had died in the process of giving birth. The pregnant uterine horn was abnormally large and was compressing the right crus of the diaphragm, resulting in significant pressure atrophy. For the otter whose transmitter was found in the tide pool, no primary cause of death could be determined, although the short time between observing the animal alive and retrieving the transmitter may implicate trauma of some sort as a primary or contributing factor.

Discussion

Significant pathological findings were detected at necropsy in all 16 otters included in this long-term life history analysis. This finding is surprising, unusual and very fortuitous, given that some carcasses were presented for necropsy in moderate to advanced postmortem decomposition and with significant postmortem scavenging. Although the level of pathological investigation could not be equivalent for all necropsied otters due to carcass limitations, clear causes of death or at least generalized disease processes were strongly suspected or confirmed for all otters with some part recovered for necropsy, with the exception of one otter whose VHF transmitter was recovered lying alone in a tide pool.

The sample population was evenly split between males and females, but was composed predominantly of adult and aged adult otters (87.6%). Previous studies have demonstrated significant associations between sea otter age class at the time of necropsy and some specific causes of death such as acanthocephalan peritonitis and mating trauma (Thomas et al., 1996; Kreuder et al., 2003). Thus trends in mortality observed in this small sample population at present may not reflect the wild population as a whole. The nutritional condition in the sample population had some understandable association with the chronicity of the most significant disease processes detected at necropsy: Three of the four otters with moderate to abundant subcutaneous fat had acute disease (shark bite, boat strike and suspected domoic acid intoxication) as primary causes of death, while over half of the otters in poor nutritional condition had more chronic lesions such as chronic heart disease or acanthocephalan peritonitis.

Examination of demographic patterns of carcass retrieval suggest that careful consideration of possible bias in carcass recovery is warranted. In the present study, 93.8% of sea otter carcasses (15 of 16 otters) were recovered from the southern half of the sea otter range, and 75% of the carcasses (12 of 16 dead otters) were recovered within 50 km of each other in the vicinity of San Simeon, California. This could represent a high-risk area for sea otter mortality worthy of further study. However, since a large proportion of the field staff tasked with daily monitoring of the tagged otters and carcass recovery were based in San Simeon, it is equally plausible that variation in monitoring effort and speed of carcass identification and recovery could have contributed to the high rate of carcass recovery in the greater San Simeon area. Careful consideration of the proportion of tagged otters confirmed dead through carcass recovery versus those lost to further follow up for the potential “high risk” (San Simeon) area compared to other study areas may help to clarify this potential source of bias. These data will also be useful for quantifying “normal” carcass recovery rates.

Detection of >1 significant lesion at necropsy is a common finding in southern sea otters (Kreuder et al., 2003), thus careful consideration of all available data is critical when studying causes of mortality. At least two otters from this study had two significant, but distinct processes at necropsy: One otter with acanthocephalan peritonitis leading to sepsis also had moderate to severe chronic cardiac disease that was superimposed on subacute cardiac pathology attributable to sepsis. In addition, an otter that died with vaginal perforation and pneumoabdomen also had moderate, pre-existing protozoal meningoencephalitis associated with the presence of *T. gondii* tissue cysts in the brain. This otter was also seropositive for *T. gondii* and the parasite was isolated from brain tissue at cell culture. However, since the immediate cause of death was associated with mating trauma, severe pneumoabdomen and inability to forage, this finding was listed as the primary cause of death. However, as both cardiac disease and protozoal meningoencephalitis can be chronic, dehabilitating diseases in sea otters, both otters likely suffered some contributory negative effects from these concurrent processes.

Protozoal infections were not significant finding in this sample of otters, possibly due to small sample size or because many of the carcasses were obtained from areas less likely to be a high-risk site for protozoal-related infection and mortality (Miller et al., 2002b; Kreuder et al., 2003). In previous studies these high-risk areas were dermined to be in the general vicinity of Morro Bay and Moss Landing, California. However, a large proportion of the live-sampled otters were seropositive to *T. gondii* and *S. neurona*, suggesting high levels of natural exposure. In previous studies, 62% of freshly dead California otters and 42% of live-sampled, presumably healthy otters were seropositive to *T. gondii*, and the proportion of seropositive otters increased significantly with advancing age (Miller et al., 2001b, 2002). Thus because over 86% of the otters in this sample group were adults or aged adults, finding high proportions of seropositive otters is not unexpected. However, infection with these parasites could pose an additive health risk if these otters face immunosppressive health threats after becoming chronically infected with protozoa. One otter is suspected of intoxication by domoic acid (DA), a natural marine biotoxin produced by algae in the genus *Pseudo-nitszchia*. The animal was recovered in an advanced state of decomposition, so intoxication could not be definitively confirmed. However the gross findings, location and time of death are supportive of DA intoxication. In addition, one of 2 postmortem diagnostic tests was positive for low to moderate levels of domoic acid. In addition, cardiac disease, as reported in several otter otters in this study, has been linked epidemiologically to prior domoic acid exposure, as well as other specific risk factors (Kreuder et al., in press).

Detailed postmortem examination of electronically tagged sea otters with extensive life history information provided an unprecedented opportunity to begin to determine patterns of disease occurrence in free-living otters, to examine these patterns in the context of extensive life history information and to compare trends observed in live-sampled otters to see if they are similar or different than those established through study of stranded carcasses. Overall, the primary causes of mortality in the live-sampled otters from this study appear to be similar to those that have been previously reported from studies of stranded otters. For example, common causes of mortality in the live sampled otters, such as acanthocephalan peritonitis, cardiac disease, gastrointestinal disease and shark bite have been documented as common causes of mortality in stranded otters. However, the sample size of 16 live otters that have died and were necropsied to date is too small at the present time to make

statistically valid comparisons of mortality trends for tagged otters, when compared to similar trends derived from analysis of hundreds of stranded otters over the past 12 years. However, this study and the subsequent follow-up will greatly facilitate those efforts. More importantly, this data provides for the first time the opportunity to begin to glimpse relationships between sea otter behavior and life history parameters, (e.g. home range size and location, dive depths and prey choices, reproductive history) and related factors such as pathogen exposure history, nutritional condition, lifespan and specific cause of death.

A complete postmortem examination by a veterinary pathologist will provide detailed information on causes of death and overall patterns of mortality in the sample population. In addition, these examinations permit a glimpse into the reproductive biology and life history of affected animals. The present study takes these examinations to a new level: linking information gained from necropsy with details on antemortem foraging history, serology, contaminants testing and locational data provides a unique opportunity to follow individual life histories and to observe patterns of disease exposure and transmission relative to location, diet and lifestyle. Previous studies of sea otter pathology have indicated that infectious agents such as parasites and bacteria play a major role as primary or contributing factors in southern sea otter mortality. Initial findings from this study appear to support those earlier findings, despite the fact that much of the sample population was composed of aged adults, a portion of the population that was found least likely to die of infectious disease (Kreuder et al., 2003). With the exception of shark-related mortality and mating trauma, many leading causes of death in this and in previous studies were recently recognized as new and important causes of mortality in southern sea otters (Thomas et al., 1996; Kreuder et al., 2003). Further analysis of this data will provide much insight into the association between the specific cause of death and key life history factors. Over time these findings could help ecologists to optimally focus their efforts and resources, to determine likely consequences of exposure to specific anthropogenic inputs, and to mitigate their effects.

Chapter 11. Summary and Synthesis

James A. Estes, M. Tim Tinker, and Katherine Ralls

Some species capture the interests of humans more strongly than others. Viewed by many as the coastal ocean's poster child, the sea otter is one such species. However, sea otters also are important for scientific reasons. They are a keystone species (Paine 1969, Power et al. 1969), functionally important because of their high per capita interaction strength (Berlow et al. 1999). The sea otter's keystone role arises from its limiting influences as a predator on various invertebrate prey, including herbivorous sea urchins. When otters are lost from coastal ecosystems, kelps and other species of macroalgae are reduced by the abundant herbivores that develop in their absence (Estes and Duggins 1995). This trophic cascade (sensu Paine 1980, Carpenter and Kitchell 1993) has a broad range of indirect effects on other coastal species and ecosystem processes (Estes 1996, Estes et al. 2004).

Coastal oceans are arguably among the most vulnerable habitats to human development. Humans live by the sea in disproportionately large numbers and the coastal oceans are the ultimate receptacles of urban, industrial and agricultural effluents. Furthermore, the coastal oceans are heavily utilized for recreation and food, and as a transport medium for the goods and materials needed to fuel a growing global economy. As a high-trophic level predator, sea otters may be more vulnerable to these activities than most other species, and as such may be bellwethers of the health of California's coastal oceans. Fortunately, sea otters also are relatively easy to study. Their numbers can be counted to provide information on trends in distribution and abundance. They can be captured and tagged, thus providing the opportunity to look closely into the lives of individuals. Dead otters commonly strand on California's beaches, thus providing valuable information on the causes of mortality. Sea otters seldom range far from land and they invariably return to the ocean's surface to consume their prey after a foraging dive. Finally, sea otters can be maintained in captive environments, thus making them amenable to experimental study.

Before the work reported in the preceding chapters of this report was initiated, a considerable body of information was available on the natural history and ecology of sea otters from California and elsewhere. General life history patterns were known from studies of stranded carcasses and living populations. The following bulleted list is a brief synopsis of the background knowledge.

- Sex ratio at birth is about 50:50.
- Sea otters are polygynous and bimaturistic, with females and males respectively reaching sexual maturity at about 3 and 5 years.
- Maximum longevity is about 20 years.
- Litter size is almost invariably one.
- Sexually mature females enter estrus immediately upon weaning or loosing their pups.

- Age-specific birth rate does not vary with population status or environmental condition (Monson et al. 2000) – population growth and decline is therefore controlled solely by variation in age and sex-specific mortality.
- The theoretical maximum rate of population increase (r_{max}) for sea otters is about 17-20 % yr^{-1} (Estes 1990). Sustained periods of population increase at or near r_{max} had been chronicled for sea otter populations in Washington, British Columbia, and at various locations in Alaska (Estes 1990).

The aforementioned information provides the necessary backdrop for asking questions about and interpreting trends in the distribution and abundance of southern sea otters. Based on current population density and habitat availability, the historical carrying capacity of sea otters in California is estimated at about 16,000 individuals (Laidre et al. 2001). If, like sea otter populations elsewhere, the southern sea otter had increased at r_{max} at the end of the fur trade, it would have reached carrying capacity by the late 1940s, more than 50 years ago (Figure 71).

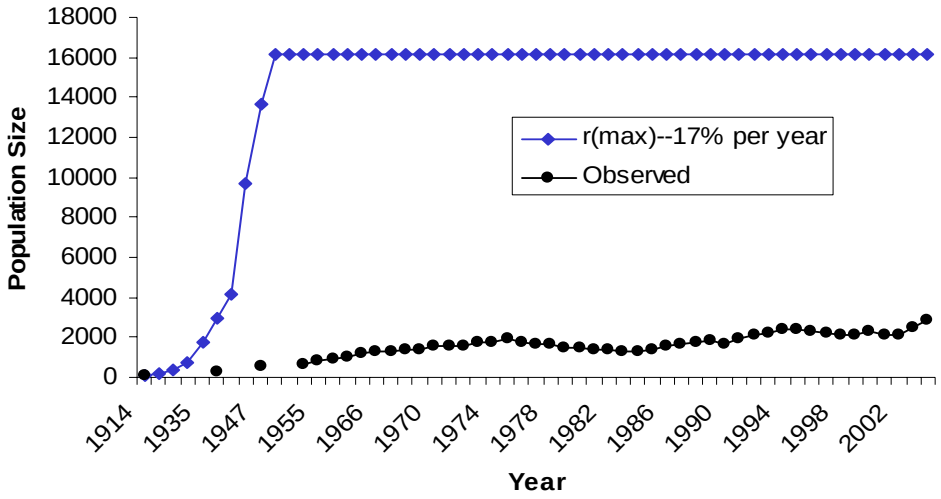

Figure 71. Trends in overall abundance of the southern sea otter population (circles) and a crude estimate of what this trend would have looked liked if the population had increased at a rate of 17% yr^{-1} to an overall carrying capacity of 16,000 animals for the state waters of California (diamonds).

Perhaps the most vexing question is why the southern sea otter population did not increase more rapidly? Even in the early part of the 20th century, when California's human population was some 20-fold less than it is today, the southern sea otter population was growing at a rate far below r_{max}. Another perplexing pattern is the recent periods of stability or decline. Although census data are sparse for the first half of the 20th century, the population marched steadily upward during this period at about 5% yr^{-1}. Prolonged periods of either higher or lower growth rates are unlikely. Hence, recent departures from the long term growth trend are a novelty, indications of fundamental change in the way the population is being influenced by its habitat. A third puzzling feature of population change in southern sea otters is that range expansion has occurred more rapidly to the south than it has to the north. This trend is not the wished-for state of affairs by natural resource users and management

agencies. Southward range expansion takes sea otters into areas where they are not permitted by federal law. Range expansion to the south also puts sea otters at elevated risk to oil and gas development, and into an environment that is more heavily utilized and impacted by human activities than either central or northern California. At the present study's onset, we knew that trends in abundance were driven by variation in mortality. Hence our focus was on survival and mortality. We also understood that the north-south inequality in range expansion must somehow relate to the interplay between mortality and movement.

Our broad goal was to understand these three patterns—the prolonged sluggish population increase, the more recent periods of population increase and decline, and the greater rate of range expansion to the south. Our efforts to achieve this goal required integrated and collaborative research in four scientific disciplines—population biology, behavior, physiology, and the veterinary health sciences. Demographic analyses were the centerpiece of our effort, for the obvious reason that changes in age and sex-specific birth and death rates are always the proximate drivers of population change. Studies of behavior and physiology were conducted to better understand the causes of mortality. The behavioral studies focused on two general topics—foraging and movements. Foraging studies were undertaken because food is an important link between any species and its environment, and in the otter's specific case, food resource availability is a key factor in limiting population growth. The physiological studies focused on energetics and thermoregulation. Energy is the common currency linking a consumer's performance with prey quality. Body temperature and thermoregulation reflect energy utilization and demand by the consumer on one hand, and the energy-extractive capacity of the environment on the other. In the otter's case, these processes appear to be both extreme and critical. As mustelids and marine mammals, sea otters "run hot", which is to say that they have elevated basal and field metabolic rates (Costa and Williams 1999). On the other side of the equation, sea otters have a high surface to volume ratio; they live in an extremely cold, heat-extractive environment; and they employ a primitive means (their fur) of insulating themselves from the cold ocean—all features that draw energy from the animal at a high rate. The health studies provided two important dimensions to our overall effort. First and foremost, they gave us detailed information on the death assemblage, including the number of animals found dead on the beach, cause of death, and how these varied by age, sex, location, and time. These data were important inputs for our demographic analyses. In addition, health profiles were obtained from living animals at the time of capture or recapture during the tagging operations.

Besides asking the right question, the most difficult aspect of any ecological study is framing that question in a dynamical perspective. Descriptions of static systems provide little or no insight into the ways things work (May 1973). We attempted to cast sea otter demography into a dynamic perspective by contrasting patterns in space and time. The spatial contrasts involved different parts of the sea otter's range—areas we knew or suspected to differ in local sea otter population status. The area near Cambria had been occupied by otters for many years and thus we thought it would be at or near equilibrium with limiting resources. We viewed the Monterey Peninsula in a similar way. In contrast, the area south of Point Conception had only recently been invaded by sea otters, and thus resources in that area were expected to be less limiting. We also have comparable information from the reintroduced sea otter population at San Nicolas Island, although field work there is only now being completed and thus the data are not available for inclusion in this report. We also

attempted to cast the sea otter system into a dynamic perspective by making contrasts in time. Data gathered during the earlier MMS-supported study by Siniff and Ralls (1988) characterize demography and behavior (physiological and health related studies were not conducted) at a time when the California sea otter population was growing. Therefore, these data provide an interesting point of comparison with the present, and an independent means of inferring differences between a population that was growing and one that was stable or in decline.

The following sections of this final chapter provide synopses of our main findings. These synopses are followed by a synthesis of what we have learned and what we believe it means.

Demography

Our demographic analyses were constructed from carcass records (variation in number, age and sex composition through time), surveys of the living population, and information on reproduction, mortality and movements from tagging and telemetry studies. Overall patterns of mortality in southern sea otters are remarkably different from those reported for sea otters elsewhere. Substantial numbers of animals die throughout the year in California, whereas elsewhere most mortality occurs during late winter/early spring. Carcass recovery records indicate that mid-summer is the period of highest mortality in California, and that the relative rate of summer mortality is more pronounced during periods of population decline than it is during periods of population increase (Estes et al. 2003a). A second oddity in California is the relatively high probability of death in prime age females. The typical pattern elsewhere is elevated mortality in post-weaning and aged individuals, but extremely low mortality rates in prime-age animals.

Our data and analyses indicate a long-term decrease in survival from the late 1980s or early 1990s to the present, and that survival rate is currently lowest in the north-central portion of the sea otter's range. The greatest reduction in survival rate was for adult females (those ≥ 4 years of age), that component of the population with the highest reproductive value. While female survival rate has declined, that of males apparently has either remained the same or increased. Thus the population sex ratio has shifted toward males. These findings are in keeping with patterns seen in the living population. That is, although recent surveys indicate an overall population increase, this increase appears to be comprised largely or entirely of males and juvenile females. The adult female component of the population apparently has remained static or declined over the same time period.

Movements and spatial ecology

The demographic analyses in conjunction with information on movements of individual sea otters provide new insights into the spatial ecology of the southern sea otter population. Re-sightings of tagged and telemetered animals confirmed the 1980s findings that, on average, sub-adults move greater distances than adults and males move greater distances than females. There were no clear differences in movement patterns between the 1980s study and the present study. However, home range size appears to have declined over this time period and the movements of animals in the Cambria area during the present study are substantially

different from those in the Monterey Peninsula area and those recorded during the 1980s study (neither of which differed from one another). These analyses indicate that sea otters in the southern half of the range during the present study moved in a more "directional manner"; that is, they were more likely to make non-random, sustained movements in one direction, consistent with long-distance movements between multiple home ranges. This pattern is likely related to the different rates of range expansion and seasonal use of habitat between the southern and northern ends of the population's range. Although the reasons for these differences remain unclear, we were able to join the movements and demographic data in stage-based projection matrices to develop a spatially structured matrix model for predicting population growth and range expansion to the south. This exercise suggested that future population increase to the south will exceed that of the remainder of the population because of immigration and a high intrinsic rate of population growth; that population expansion to the south is most sensitive to dispersal and survival of juvenile and sub-adult females; and that overall population growth is most sensitive to the survival of females in the center of the range. These analyses and findings provide a useful tool for assessing alternative management options. They also identify key life history parameters that require further study in order to improve the precision of population projections.

Diet

We have obtained major new insights into the diet and foraging behavior of sea otters, and how variation in these aspects of natural history may be related to fitness and population status. Our work in this arena had three main dimensions—diet, activity budgets, and diving behavior. Our earlier work showed that most sea otters have narrow and highly individualized diets, which appear to be passed across generations through matrilineal learning (Estes et al. 2003b). The present study exposed even more startling patterns of individuality. Multivariate statistical analyses revealed that individual dietary patterns cluster in three distinct groups, each with its own unique dive and prey capture efficiency, average net rate of energy gain, and variance in net rate of energy gain. At one extreme are individuals that are risk-averse (low net rate of energy gain, but with little variation around the average because of the low margin for error). At the other extreme are individuals that appear more risk-inclined (higher net rate of energy gain, but with greater variation around the average because of the higher margin for error). These general patterns appear to be alternate solutions to the problem of dealing with food resource limitation.

Diving and activity budgets

The archival TDR's provided a highly detailed and unbiased view of diving behavior that could be combined with dietary information. Dive pattern and dive depth were found to vary by sex, area, and among the three general foraging types. Males were deeper divers than females; the risk-averse females tended to have shorter post-dive intervals than risk-inclined females; and both dive depth and post-dive duration were longer for males when they were south of Point Conception than when they were in central California. Activity budgets were difficult to interpret because of the high degree of individual variation. In general, males that moved between the area southeast of Point Conception and central California tended to have shorter foraging bouts and to spend less time foraging when they were south of Point Conception. Overall, the time spent foraging appears to have increased since the 1980s

study. Taken together, these findings suggest that food resource accessibility influences time spent foraging in sea otters, and that food resources are less available to sea otters in central California now than they were during the 1980s.

Energetics and thermoregulation

Mammalian predators have relatively high energy requirements compared with other vertebrates, and even other homeotherms. Foraging mode varies substantially among species, depending on body size and habitat. Small body size and the cold marine environment appear to have constrained the sea otter to forage frequently for short periods, especially compared with large terrestrial carnivores. Energy acquisition and loss are both high in sea otters. Body temperatures in these animals were found to vary considerably through time—by as much as 2 ^{o}C within a 24 hr period. The core temperature measurements from wild otters indicate that they are incapable of maintaining a constant body temperature while in the resting state. This thermal draw-down in resting animals appears to limit the duration of resting to several hours. Otters typically forage intensively prior to resting. The heat gain during this period results from exercise, tissue metabolism, and digestion. Our extensive observations of captive and wild diving otters indicate that heat balance and thermal flux place significant constraints on their behavior. The thermal costs of different behaviors varied substantially. Grooming, the most energetically costly behavior, is essential for longer-term thermoregulation. Swimming and diving are also energetically costly. The high energy demands of adult males associated with extensive surface swimming and their increased body size relative to females may help explain why males periodically migrate to the comparatively food-rich area south of Point Conception. These findings and speculations suggest that various aspects of behavior and activity in the sea otter are shaped, or at least constrained by their energetic and thermal requirements.

Health and disease

Living sea otters showed little evidence of health problems whereas a substantial proportion of the dead ones succumbed to various forms of infectious disease. Almost half of the fresh sea otter carcasses that have been necropsied over the past 12 years died from some form of parasitic infection or microbial disease. Infectious disease is a leading cause of death in southern sea otters and is thus an important limiting factor in population growth. Given these conclusions, one might expect to see some signs of ill health in the living population. To date, this has not been the case. In general, living sea otters show no signs of chronic health problems, at least based on blood chemistry and hematology, immune function, and other diagnostic procedures. However, there is still a considerable amount of work to be done on contaminant burdens, nutrition, immune function, and genetics. At this point we must conclude that infectious disease is a significant demographic driver of the southern sea otter population, although the degree to which this reflects a disease-rich environment or increased vulnerability due to food limitation, immune dysfunction, or some interactive effect of these factors remains unknown.

Syntheses

Findings from this study have sharpened our view of spatial structure in the southern sea otter population. The tagging studies confirm what we have long known—that adult sea otters have strong affinities to particular locales and that these affinities are usually maintained throughout their lives even though individual otters sometimes move long distances. We have recorded cases of individuals moving from one end of the range to the other over relatively short time periods. These movements provide a means of internal connectivity to the entire southern sea otter population--the potential for gene flow, disease transfer, and any other feature that might be carried by an individual through a population as it moves through space and time. Our findings also revealed a larger scale pattern of spatial structure in the southern sea otter population--a significant difference in behavior and demography between animals that live at the northern and southern ends of the range. Sea otters at the southern end of their range appear to be less limited by resource availability than they are in the north or range center. Overall survival rates also are somewhat higher in the south than they are in the north. Movement patterns differ significantly between these two regions. Males throughout the range move to the southern range periphery during the late winter and early spring. The precise reasons for these movements are still uncertain, although we now have considerable evidence to suggest that access to increased food availability at the southern range periphery is a likely motivation, and is certainly a beneficial nutritional consequence. Other potential causal factors include interactions with females or other males within their traditional home ranges (Jameson 1989), although in the case of radio-tagged males that occasionally traveled to the range periphery we saw no evidence of exclusion from territories by other males, and in fact when they did return north they immediately reclaimed their previous territories. Whatever the proximate reasons for these movements, we see the benefits reflected in improved body condition, reduced foraging behavior, and increased survival.

The perplexing unanswered question is why this behavior—back and forth movement from the range periphery—is so asymmetric between the northern and southern ends of the range. Comparable behavior does not appear to occur in the north, despite the existence of seemingly similar patterns of population structure and food availability. Monterey Bay has been invoked by some as a barrier of sorts to movement, but this explanation fails to account for the historical pattern of slower range expansion to the north (Riedman and Estes 1990), and is also inconsistent with the large numbers of animals counted in Monterey Bay during recent surveys. At this time we can provide no obvious explanation for this north/south discrepancy. But regardless of cause, the pattern has important consequences because it has created a rapid southward expansion of the range of the southern sea otter and it apparently results, at least to some degree, in greater food resource limitation and higher mortality rates in the north than in the south.

We knew at the onset of this study that variation in mortality was the major demographic driver in sea otter population change. Unlike some terrestrial carnivores (Fuller and Sievert 2001) sea otters rarely, if ever, skip mating opportunities, reabsorb their embryos or fetuses, or delay the age of first reproduction in response to reduced prey availability. Instead, population regulation is achieved through variation in post-partum survival. Monson et al. (2000) proposed that this is a bet-hedging strategy, driven by low environmental

predictability, a relatively low cost of pregnancy, and the high cost of post-partum care. A key decision point for individual females is whether or not to invest further in their offspring at the time of birth. This would explain the high mortality rate of pups shortly after birth (Siniff and Ralls 1988, Reidman *et al.* 1994) and the large number of orphaned pups—presumably reflections of a female's decision to abandon her current reproductive investment to favor her own survival and lifetime fitness. The large numbers of orphaned pups at the northern end of the range is consistent with our findings—that resource limitation is most acute in this general area. However, it is also abundantly clear that adult mortality, especially through the prime age classes, contributes significantly to the population trajectory. Collectively, this elevated mortality must explain why the southern sea otter population has never increased at a rate comparable to that of populations elsewhere. Adult mortality is a major component of this overall mortality, for which there appears to be a wide range of causes, the most important of which is infectious disease. On the other hand, the more subtle changes in population trajectory are more difficult to understand because they involve subtle changes in mortality. We simply do not have a monitoring program in place that is sensitive enough to detect such subtle changes in mortality. Hence, with the exception of some temporary declines likely due to incidental take in fisheries (Estes et al. 2003a) we have no understanding of why the population has waxed and waned over the past several decades. This is a key issue because mitigating the reasons for these subtle changes will determine if the southern sea otter population is to recover or decline toward extinction.

Where should research in the Threatened southern sea otter proceed from here? Continued monitoring is essential but counts of the living population and assessments of the numbers and causes of death in beach-cast carcasses are not enough to provide anything more than general trends in abundance and mortality. The number of beach-cast carcasses collected per unit time has been interpreted in the past as an index of population health or status, but more recently we have found that relative number of recovered carcasses provides little predictive value for forecasting population trends. The spatially explicit nature of mortality, the confounding effects of unequal carcass recovery rates in different portions of the range, and age/sex bias in specific causes of mortality all serve to preclude the interpretation of population status based on carcass collection alone. In view of this limitation, three areas of future study seem warranted. One is continued monitoring of individual sea otters through tagging and telemetry. A more careful focus on living animals and how they transition from life to death is an important adjunct to monitoring of the dead ones. Further examination of the data collected in this study, and exploratory exercises using the population modeling infrastructure developed herein, will be critical for determining where to focus such monitoring efforts, at what level of intensity, and for which age/sex classes.

A second area of further research should focus on prey quality and availability on the one hand and the foraging behavior of sea otters on the other. We still do not fully understand the significance of dietary individuality, either at the level of the individual or the level of the population. Future research should strive to understand why sea otter foraging behavior aggregates in three foraging types, whether or not variation in foraging behavior affects body condition, diet quality, disease susceptibility, survival, and reproduction, and whether or not this kind of behavior occurs elsewhere in sea otters, and if so (or not), why.

Finally, future research on the southern sea otter and its associated ecosystem must continue to focus on health and infectious disease. It is abundantly clear on the one hand that disease issues are immensely important to the long-term welfare of the southern sea otter. On the other hand, we have little understanding of disease ecology in this system. Is infectious disease in the southern sea otter an emergent phenomenon, destined to get worse, or a long-term feature of central California's coastal ecosystem? What are the real causes of so much disease-related mortality in the southern sea otter? Are they mainly due to exposure levels – that is, an environment with high levels of parasites and pathogens – or to a population of sea otters that is especially vulnerable to infectious disease because of nutritional stress (Calder et al. 2002), contaminants and/or inbreeding depression, or some combination of these factors? This is an extremely important question because mitigation would be vastly different under the two scenarios. We still need to better understand the extent to which infectious disease is an ultimate vs. proximate cause of death. Further analyses of the data collected in this study from individual study animals, with the aim of linking cause of death (especially for those animals that died from disease) with diet, reproductive history, behavior and other risk factors, will allow us to begin to address these difficult questions. Finally, while disease is clearly important, it may never be easy or even possible to mitigate. Thus, we must pay more attention to quantifying other causes of mortality because these may be the more manageable foci of effective short-term management.

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Appendix A:

Appendix A. Maximum Likelihood analysis of carcass distributions and population counts, 1992-2001: summary of 34 model forms having greatest support ($\Delta i \leq 5$)

Model Support		Model Description							
AIC	a_i	Sex Effect[1]	Wean Rate	Time Effect[2]	Time Effect Interactions	Number Spatial Groups	Grouping Configuration[3]	Location Effect Interactions	Interaction Explanation
472.63	0.127	simple	baseline	categorical	time-age	2	1122	none	time effect increases with age
474.04	0.063	simple	baseline	continuous	none	2	1122	none	
474.12	0.060	simple	lower	none	none	2	1122	none	
474.23	0.057	age-sex	baseline	none	none	2	1122	none	
474.30	0.055	simple	baseline	none	none	1	1111	none	
474.62	0.047	simple	baseline	continuous	time-sex	2	1122	none	time effect greater for females
474.64	0.047	simple	baseline	none	none	2	1122	none	
475.07	0.038	simple	baseline	none	none	2	1211	none	
475.10	0.037	simple	baseline	continuous	none	2	1211	none	
475.43	0.031	simple	baseline	none	none	2	1122	group-age	juv./subadult survival higher in south
475.43	0.031	simple	baseline	categorical	none	2	1211	none	
475.52	0.030	simple	baseline	none	none	3	1231	none	
475.76	0.027	simple	lower	categorical	none	2	1122	none	
475.77	0.026	age-sex	baseline	none	none	3	1231	none	
475.93	0.024	simple	lower	continuous	none	2	1122	none	
476.03	0.023	age-sex	baseline	categorical	none	2	1122	none	

Appendix A. (continued)

AIC	a_i	Sex Effect[1]	Wean Rate	Time Effect[2]	Time Effect Interactions	Number Spatial Groups	Grouping Configuration[3]	Location Effect Interactions	Interaction Explanation
476.27	0.021	simple	baseline	categorical	none	2	1122	none	
476.36	0.020	simple	baseline	continuous	group-time	2	1122	group-time	time effect not as strong in south
476.37	0.020	age-sex	lower	none	none	2	1122	none	
476.42	0.019	age-sex	baseline	continuous	none	2	1122	none	
476.68	0.017	simple	baseline	continuous	time-age	2	1122	none	time effect increases with age
476.86	0.015	age-sex	baseline	none	none	2	1211	none	
476.92	0.015	age-sex	baseline	continuous	group-time	2	1122	group-time	time effect not as strong in south
476.94	0.015	simple	time intxn	continuous	none	2	1122	none	weaning succes increases with time
476.96	0.015	simple	lower	none	none	3	1231	none	
476.97	0.015	simple	baseline	categorical	time-age	2	1211	none	time effect increases with age
476.99	0.014	age-sex	lower	continuous	none	2	1122	none	
477.05	0.014	age-sex	baseline	categorical	none	2	1211	group-age	juv./subadult survival higher in south
477.08	0.014	age-sex	baseline	continuous	none	2	1211	none	

Appendix A. (continued)

AIC	a_i	Sex Effect[1]	Wean Rate	Time Effect[2]	Time Effect Interactions	Number Spatial Groups	Grouping Configuration[3]	Location Effect Interactions	Interaction Explanation
477.11	0.014	simple	baseline	categorical	group-time	2	1122	group-time	time effect not as strong in south
477.14	0.013	simple	baseline	continuous	time-sex	2	1211	none	time effect greater for females
477.27	0.013	simple	lower	continuous	group-time	2	1122	group-time	time effect not as strong in south
477.38	0.012	age-sex	lower	continuous	group-time	2	1122	group-time	time effect not as strong in south
477.60	0.011	simple	lower	none	none	2	1211	none	

[1] Simple effect of sex indicates lower male survival relative to females for all ages; age-sex interaction indicates greater decrease in survival with age for males relative to females

[2] Time effect, when present, was always negative (decreased survival from 1992 to 2001). For categorical time effects, location of temporal break was 1994-95 in all cases

[3] Grouping levels are shown for the 4 major geographic sub-divisions: 1) northern periphery, 2) north-center, 3) south-center and 4) southern periphery of range. Thus a code of "1122" indicates that geographical sub-divisions 1 and 2 were grouped together (i.e. had identical demographic rates) but were different from sub-divisions 3 and 4.

Appendix B:

Appendix B. Sea otter survival rates[1]: Maximum Likelihood model-averaged estimates for 1992-2001

1. Northern Periphery of Range

	Juvenile (0-1 years)				Subadult (2-3 years)				Adult (4-10 years)				Old Adult (11-20 years)			
Year	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95
Females																
1992	0.858	0.0316	0.784	0.910	0.869	0.0128	0.842	0.892	0.870	0.0171	0.833	0.900	0.556	0.1899	0.217	0.850
1993	0.857	0.0312	0.784	0.908	0.867	0.0124	0.841	0.890	0.869	0.0176	0.830	0.899	0.553	0.1910	0.214	0.849
1994	0.855	0.0308	0.784	0.906	0.866	0.0124	0.839	0.888	0.867	0.0185	0.826	0.899	0.550	0.1921	0.210	0.848
1995	0.849	0.0311	0.777	0.900	0.858	0.0132	0.830	0.882	0.855	0.0236	0.802	0.896	0.527	0.2025	0.185	0.845
1996	0.847	0.0308	0.776	0.898	0.856	0.0134	0.828	0.881	0.853	0.0245	0.799	0.895	0.524	0.2036	0.182	0.845
1997	0.845	0.0307	0.775	0.896	0.855	0.0140	0.825	0.880	0.851	0.0256	0.794	0.895	0.521	0.2047	0.179	0.844
1998	0.844	0.0306	0.774	0.895	0.853	0.0152	0.821	0.880	0.849	0.0268	0.789	0.895	0.518	0.2058	0.176	0.844
1999	0.842	0.0308	0.772	0.893	0.851	0.0166	0.816	0.881	0.847	0.0283	0.783	0.895	0.515	0.2070	0.173	0.843
2000	0.840	0.0313	0.769	0.892	0.849	0.0182	0.810	0.882	0.845	0.0299	0.777	0.895	0.512	0.2083	0.170	0.843
2001	0.838	0.0321	0.765	0.892	0.847	0.0199	0.804	0.882	0.843	0.0317	0.771	0.896	0.509	0.2095	0.167	0.843
Males																
1992	0.809	0.0327	0.736	0.865	0.811	0.0204	0.768	0.848	0.784	0.0352	0.707	0.845	0.371	0.1673	0.127	0.706
1993	0.807	0.0318	0.737	0.861	0.809	0.0200	0.767	0.845	0.782	0.0349	0.706	0.842	0.368	0.1672	0.125	0.705
1994	0.805	0.0311	0.736	0.858	0.807	0.0201	0.765	0.843	0.779	0.0350	0.703	0.840	0.365	0.1673	0.123	0.703
1995	0.796	0.0287	0.734	0.847	0.797	0.0197	0.756	0.833	0.763	0.0413	0.673	0.834	0.345	0.1707	0.107	0.698
1996	0.794	0.0284	0.733	0.844	0.795	0.0203	0.752	0.832	0.760	0.0414	0.670	0.832	0.342	0.1707	0.105	0.697
1997	0.792	0.0285	0.730	0.842	0.792	0.0215	0.747	0.831	0.757	0.0420	0.666	0.830	0.339	0.1708	0.103	0.696
1998	0.790	0.0291	0.727	0.841	0.790	0.0231	0.741	0.832	0.754	0.0430	0.661	0.829	0.336	0.1709	0.102	0.695
1999	0.787	0.0300	0.723	0.840	0.787	0.0250	0.734	0.832	0.752	0.0445	0.655	0.828	0.334	0.1711	0.100	0.694
2000	0.785	0.0313	0.717	0.840	0.785	0.0271	0.727	0.833	0.749	0.0462	0.648	0.828	0.331	0.1713	0.098	0.693
2001	0.782	0.0328	0.711	0.840	0.782	0.0293	0.719	0.834	0.746	0.0483	0.640	0.828	0.328	0.1715	0.096	0.692

[1] Weaning success rates were approximately constant over time and across areas, adult mean = 0.61, SE = 0.067, 95% CI = 0.48–74

Appendix B. (continued)

2. North-Center of Range

	Juvenile (0-1 years)				Subadult (2-3 years)				Adult (4-10 years)				Old Adult (11-20 years)			
Year	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95
Females																
1992	0.853	0.0330	0.776	0.907	0.864	0.0139	0.834	0.889	0.866	0.0171	0.829	0.896	0.550	0.1885	0.216	0.845
1993	0.852	0.0325	0.776	0.905	0.862	0.0133	0.834	0.887	0.864	0.0175	0.826	0.895	0.547	0.1896	0.212	0.844
1994	0.850	0.0321	0.776	0.903	0.861	0.0130	0.833	0.884	0.863	0.0183	0.823	0.895	0.544	0.1908	0.209	0.844
1995	0.843	0.0328	0.768	0.897	0.853	0.0144	0.822	0.879	0.851	0.0228	0.801	0.890	0.521	0.2006	0.184	0.840
1996	0.842	0.0323	0.768	0.895	0.851	0.0143	0.821	0.877	0.849	0.0235	0.797	0.890	0.518	0.2017	0.181	0.840
1997	0.840	0.0318	0.767	0.893	0.850	0.0146	0.819	0.876	0.847	0.0245	0.793	0.889	0.515	0.2029	0.178	0.839
1998	0.838	0.0315	0.767	0.891	0.848	0.0153	0.815	0.876	0.845	0.0257	0.788	0.889	0.512	0.2041	0.175	0.839
1999	0.837	0.0314	0.765	0.889	0.846	0.0165	0.811	0.876	0.843	0.0271	0.782	0.889	0.509	0.2054	0.172	0.839
2000	0.835	0.0315	0.764	0.888	0.844	0.0179	0.806	0.876	0.841	0.0288	0.776	0.890	0.506	0.2066	0.169	0.838
2001	0.833	0.0319	0.761	0.886	0.842	0.0196	0.800	0.877	0.839	0.0305	0.770	0.890	0.504	0.2079	0.166	0.838
Males																
1992	0.802	0.0321	0.732	0.858	0.805	0.0199	0.763	0.841	0.778	0.0353	0.702	0.840	0.365	0.1631	0.127	0.696
1993	0.800	0.0309	0.733	0.854	0.803	0.0190	0.763	0.838	0.776	0.0348	0.700	0.837	0.362	0.1630	0.125	0.694
1994	0.798	0.0300	0.733	0.851	0.801	0.0188	0.761	0.835	0.773	0.0347	0.698	0.834	0.359	0.1631	0.123	0.692
1995	0.790	0.0277	0.730	0.839	0.791	0.0191	0.751	0.826	0.757	0.0404	0.669	0.827	0.339	0.1659	0.107	0.686
1996	0.788	0.0269	0.730	0.836	0.788	0.0195	0.747	0.824	0.754	0.0403	0.667	0.824	0.336	0.1658	0.105	0.685
1997	0.785	0.0266	0.729	0.833	0.786	0.0205	0.743	0.823	0.751	0.0406	0.663	0.822	0.333	0.1659	0.103	0.683
1998	0.783	0.0268	0.726	0.831	0.783	0.0220	0.737	0.823	0.748	0.0415	0.659	0.821	0.330	0.1660	0.102	0.682
1999	0.781	0.0275	0.722	0.830	0.781	0.0238	0.731	0.824	0.745	0.0428	0.653	0.820	0.327	0.1661	0.100	0.681
2000	0.778	0.0286	0.717	0.829	0.778	0.0258	0.724	0.825	0.742	0.0445	0.646	0.820	0.325	0.1663	0.098	0.680
2001	0.776	0.0301	0.711	0.829	0.776	0.0280	0.716	0.826	0.739	0.0465	0.639	0.820	0.322	0.1666	0.096	0.680

Appendix B. (continued)

3. South-Center of Range

	Juvenile (0-1 years)				Subadult (2-3 years)				Adult (4-10 years)				Old Adult (11-20 years)			
Year	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95
Females																
1992	0.867	0.0281	0.802	0.913	0.876	0.0131	0.848	0.899	0.874	0.0179	0.835	0.905	0.554	0.1903	0.215	0.849
1993	0.866	0.0277	0.802	0.911	0.874	0.0127	0.847	0.897	0.873	0.0182	0.832	0.904	0.551	0.1911	0.212	0.848
1994	0.864	0.0273	0.801	0.909	0.873	0.0126	0.846	0.895	0.871	0.0189	0.829	0.904	0.547	0.1921	0.209	0.847
1995	0.858	0.0277	0.794	0.904	0.865	0.0131	0.837	0.889	0.859	0.0229	0.808	0.899	0.524	0.2021	0.183	0.843
1996	0.856	0.0273	0.794	0.902	0.863	0.0131	0.836	0.887	0.858	0.0233	0.805	0.898	0.521	0.2030	0.181	0.843
1997	0.854	0.0271	0.793	0.900	0.862	0.0134	0.833	0.886	0.856	0.0241	0.802	0.897	0.518	0.2039	0.178	0.842
1998	0.852	0.0270	0.791	0.898	0.860	0.0141	0.830	0.885	0.854	0.0250	0.798	0.896	0.514	0.2048	0.175	0.841
1999	0.851	0.0272	0.789	0.896	0.858	0.0151	0.826	0.885	0.852	0.0262	0.793	0.896	0.511	0.2058	0.172	0.840
2000	0.849	0.0275	0.787	0.895	0.856	0.0164	0.821	0.885	0.850	0.0274	0.788	0.896	0.508	0.2068	0.169	0.840
2001	0.847	0.0282	0.783	0.894	0.854	0.0179	0.815	0.886	0.847	0.0289	0.782	0.896	0.505	0.2079	0.167	0.839
Males																
1992	0.820	0.0278	0.759	0.868	0.821	0.0196	0.779	0.856	0.791	0.0347	0.715	0.851	0.370	0.1618	0.131	0.696
1993	0.818	0.0267	0.760	0.865	0.819	0.0190	0.779	0.853	0.788	0.0341	0.714	0.847	0.367	0.1614	0.129	0.693
1994	0.816	0.0259	0.760	0.861	0.817	0.0191	0.776	0.851	0.786	0.0338	0.712	0.845	0.363	0.1613	0.127	0.691
1995	0.808	0.0231	0.758	0.849	0.807	0.0186	0.768	0.840	0.769	0.0388	0.685	0.836	0.342	0.1640	0.111	0.684
1996	0.805	0.0226	0.757	0.846	0.804	0.0189	0.764	0.839	0.766	0.0385	0.683	0.833	0.339	0.1637	0.109	0.682
1997	0.803	0.0225	0.755	0.844	0.802	0.0198	0.760	0.838	0.764	0.0386	0.680	0.831	0.336	0.1635	0.107	0.680
1998	0.801	0.0229	0.752	0.842	0.799	0.0211	0.755	0.837	0.761	0.0392	0.676	0.829	0.333	0.1635	0.105	0.679
1999	0.798	0.0237	0.748	0.841	0.797	0.0226	0.749	0.837	0.758	0.0402	0.671	0.828	0.330	0.1634	0.104	0.677
2000	0.796	0.0248	0.743	0.840	0.794	0.0244	0.742	0.838	0.755	0.0416	0.665	0.827	0.327	0.1635	0.102	0.676
2001	0.793	0.0262	0.737	0.840	0.791	0.0265	0.735	0.839	0.751	0.0433	0.657	0.827	0.324	0.1635	0.100	0.675

Appendix B. (continued)

4. Southern Periphery of Range

	Juvenile (0-1 years)				Subadult (2-3 years)				Adult (4-10 years)				Old Adult (11-20 years)			
Year	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95
Females																
1992	0.869	0.0267	0.807	0.913	0.878	0.0118	0.852	0.899	0.876	0.0178	0.837	0.907	0.557	0.1924	0.214	0.853
1993	0.867	0.0263	0.807	0.911	0.876	0.0116	0.851	0.897	0.874	0.0183	0.834	0.906	0.554	0.1933	0.211	0.852
1994	0.866	0.0260	0.806	0.909	0.874	0.0116	0.850	0.895	0.872	0.0191	0.830	0.906	0.550	0.1943	0.208	0.851
1995	0.859	0.0266	0.799	0.904	0.867	0.0126	0.840	0.890	0.861	0.0238	0.807	0.901	0.527	0.2044	0.182	0.847
1996	0.858	0.0263	0.798	0.902	0.865	0.0127	0.838	0.888	0.859	0.0244	0.804	0.901	0.524	0.2053	0.180	0.847
1997	0.856	0.0261	0.797	0.900	0.863	0.0133	0.835	0.887	0.857	0.0252	0.800	0.900	0.520	0.2062	0.177	0.846
1998	0.854	0.0262	0.795	0.898	0.862	0.0142	0.831	0.887	0.855	0.0263	0.796	0.900	0.517	0.2072	0.174	0.845
1999	0.852	0.0264	0.793	0.897	0.860	0.0155	0.827	0.887	0.853	0.0274	0.791	0.899	0.514	0.2082	0.171	0.844
2000	0.850	0.0270	0.789	0.896	0.858	0.0169	0.821	0.888	0.851	0.0288	0.786	0.899	0.511	0.2092	0.168	0.844
2001	0.848	0.0278	0.786	0.895	0.856	0.0186	0.815	0.889	0.849	0.0302	0.780	0.899	0.508	0.2103	0.166	0.843
Males																
1992	0.822	0.0275	0.762	0.870	0.823	0.0186	0.784	0.857	0.793	0.0338	0.719	0.852	0.373	0.1635	0.131	0.701
1993	0.820	0.0265	0.762	0.867	0.821	0.0184	0.782	0.854	0.791	0.0332	0.718	0.849	0.370	0.1631	0.129	0.698
1994	0.818	0.0258	0.762	0.863	0.819	0.0188	0.779	0.853	0.788	0.0332	0.716	0.846	0.366	0.1630	0.127	0.696
1995	0.810	0.0234	0.760	0.852	0.809	0.0189	0.769	0.843	0.772	0.0383	0.688	0.838	0.345	0.1657	0.111	0.689
1996	0.808	0.0231	0.758	0.849	0.806	0.0195	0.765	0.842	0.769	0.0381	0.686	0.835	0.342	0.1655	0.110	0.687
1997	0.805	0.0232	0.756	0.847	0.804	0.0206	0.761	0.841	0.766	0.0384	0.683	0.833	0.339	0.1654	0.108	0.686
1998	0.803	0.0237	0.752	0.845	0.801	0.0219	0.755	0.841	0.763	0.0391	0.678	0.831	0.336	0.1653	0.106	0.684
1999	0.800	0.0247	0.748	0.844	0.799	0.0235	0.749	0.841	0.760	0.0402	0.673	0.830	0.333	0.1654	0.104	0.682
2000	0.798	0.0259	0.743	0.844	0.796	0.0253	0.742	0.841	0.757	0.0418	0.666	0.829	0.330	0.1654	0.102	0.681
2001	0.795	0.0273	0.737	0.844	0.794	0.0274	0.735	0.842	0.754	0.0436	0.659	0.829	0.327	0.1655	0.100	0.680

Appendix C:

Appendix C. Maximum Likelihood analysis of mark-resight survival data, 2001-2003: summary of 10 model forms having greatest support ($\Delta i \leq 10$)

Model Support		Model Description				
AIC	a_i	Sex Effect	Spatial Variation [1]	Yearly Variation	Seasonal Variation	Season-Location Interaction
254.3	0.541	No	(1 = 2) < 3	no	summer < winter & fall in areas 1 & 2	summer > winter & fall in area 3
256.6	0.172	No	(1 = 2) < 3	no	summer < winter & fall in areas 1 & 2	no seasonal variation in area 3
257.7	0.097	No	no	no	no	no
259.3	0.043	No	(1 = 2) < 3	no	no	no
259.5	0.040	males > females	no	no	no	no
259.9	0.032	No	no	no	summer < winter & fall	no
260.1	0.029	No	no	2003 < 2001 & 2002	no	no
260.9	0.020	No	2 < 1 < 3	no	no	no
261.3	0.016	males > females	(1 = 2) < 3	no	no	no
263.3	0.006	No	(1 = 2) < 3	2003 < 2001 & 2002	no	no

[1] Spatial variation effect, when present, allows for different survival estimates for three study areas: 1 = Monterey peninsula, 2 = San Simeon, 3 = Pt. Conception

Appendix D. Raw data for non-radio and radio implanted animals capture in two areas, Point Conception (ptcn) and Piedras Blancas (pbla) between March 2001 and October 2002. Data includes the following parameters: date of capture (DOC); United States Geological Survey - Biological Resource Division identification number (BRD); VHF radio identification or indication of flipper tag color combination (Name)*; sex (f = female, m = male); age class designations (ACL) (adult = adl, sub-adult = sb-a, juvenile = juv, pup = pup); age estimate in years (AYR)**; quality of age estimate (AQL)**; weight of animal (kg) at time of capture (Weight), total body length (nose-to-tail, cm) at time of capture (Length); number of resights collected per animal (Resight); most recent visual sighting of animal (Last Seen); status of animal (alive, confirmed dead (cnf dead), or presumed dead (prb dead)***); carcass identification number for recovered, deceased animals (Carcass #), identification of animals equipped with TDRs (time depth recorders, "yes" if implanted) ; and identification of animals from which TDRs were recovered

Year	Area	DOC	BRD	Name	Sex	ACL	AYR	AQL	Weight	Length	Resight	Last Seen	Status	Carcass #	TDR	TDR Rec
Non-radio implanted animals (Tagged only)																
2001	pbla	24-Mar-01	793-01	ch-bl-f	f	adl			23.45	120.00	79	15-Apr-04	unkown			
2001	pbla	24-Mar-01	794-01	ch-go	f	pup	0	A			1	24-Mar-01	unkown			
2001	pbla	24-Mar-01	795-01	ch-br	m	pup	0	A			1	24-Oct-00	dead	3514-01		
2001	ptcn	08-May-01	810-01	wh-bl	m	adl			26.00	122.50	1	08-May-01	unkown			
2002	pbla	20-Mar-02	837-02	ch-si	f	adl			18.65	112.50	9	30-Apr-03	unkown			
2002	pbla	25-Mar-02	858-02	ch-bl-m	m	juv	1	A			4	20-Nov-02	unkown			
2002	pbla	25-Mar-02	859-02	wh-ye	m	juv	1	A	25.40		3	21-Oct-03	dead	4043-03		
Radio implanted animals																
2001	ptcn	08-May-01	805-01	6-171	m	adl	5	B	29.70	132.00	64	02-Oct-03	alive		Yes	
2001	ptcn	08-May-01	806-01	6-216	m	adl	7	B	28.00	129.50	45	02-Dec-02	alive		Yes	
2001	ptcn	08-May-01	807-01	6-226	m	adl	4	B	25.70	126.00	28	29-Apr-03	alive		Yes	
2001	ptcn	08-May-01	808-01	6-242	m	adl	4	A	27.00	129.50	96	07-Apr-04	alive		Yes	
2001	ptcn	08-May-01	809-01	6-259	m	adl	4	A	30.00	123.00	295	29-Mar-04	alive		Yes	Yes
2001	ptcn	08-May-01	811-01	6-283	m	juv	1	A	22.00	120.00	34	02-Dec-03	cnf dead	4072-03	Yes	Yes
2001	ptcn	09-May-01	812-01	6-298	m	adl	5	B	29.00	132.50	33	15-Aug-03	alive		Yes	
2001	ptcn	09-May-01	813-01	6-309	m	adl	5	B	28.00	128.00	22	13-Nov-02	cnf dead	3810-02		
2001	ptcn	09-May-01	814-01	6-316	m	adl	4	B	23.00	124.00	55	19-Feb-04	alive			
2001	ptcn	09-May-01	815-01	6-332	m	sb-a	3	B	32.00	133.50	35	04-Feb-03	alive			
2001	ptcn	10-May-01	816-01	6-382	m	adl	4	B	27.00	133.50	68	19-Nov-03	alive			
2001	ptcn	10-May-01	817-01	6-356	m	sb-a	3	B	26.00	124.00	51	10-Mar-04	alive			
2001	ptcn	10-May-01	818-01	6-371	m	adl	6	B	28.00	129.50	38	21-Jan-04	cnf dead	4285-04		
2001	ptcn	09-May-01	820-01	6-268	m	adl	6	B	26.00	124.00	13	24-May-02	prb dead		Yes	
2002	ptcn	22-Apr-02	857-02	6-132m	m	adl	4	B	24.50	122.50	19	31-Mar-03	prb dead		Yes	
2002	ptcn	22-Apr-02	860-02	6-342	m	adl	6	A	31.70	128.00	18	09-Aug-03	prb dead		Yes	
2002	ptcn	22-Apr-02	861-02	6-407	m	sb-a			20.60		33	10-Mar-04	alive		Yes	
2002	ptcn	24-Apr-02	862-02	6-421	m	adl	6	B	32.00	128.00	16	15-Apr-03	prb dead		Yes	
2002	ptcn	24-Apr-02	863-02	6-433	m	adl	7	B	36.35	126.00	24	10-Mar-04	alive		Yes	
2002	ptcn	24-Apr-02	864-02	6-473	m	adl	5	B	27.00	118.50	26	10-Mar-04	alive			
2002	ptcn	24-Apr-02	865-02	6-483	m	adl	6	B	33.00	131.50	32	10-Mar-04	alive		Yes	
2002	ptcn	25-Apr-02	866-02	6-508	m	sb-a	2	B	28.00	125.00	4	31-Mar-03	prb dead			
2002	ptcn	25-Apr-02	869-02	6-597	m	adl			24.50	122.00	15	10-Mar-04	alive		Yes	Yes
2002	ptcn	22-Apr-02	871-02	6-731	m	adl	13	A	29.60	129.00	35	10-Mar-04	alive			
2002	ptcn	22-Apr-02	873-02	6-756	f	sb-a	3	B	21.00	114.50	27	10-Mar-04	alive			

Table continued

Year	Area	DOC	BRD	Name	Sex	ACL	AYR	AQL	Weight	Length	Resight	Last Seen	Status	Carcass #	TDR	TDR Rec
2001	pbla	24-Mar-01	787-01	6-008	f	adl	5	A	18.40	114.00	551	09-Feb-03	alive		Yes	
2001	pbla	24-Mar-01	788-01	6-089	f	adl	7	B	19.30	119.50	784	18-Apr-04	alive		Yes	Yes
2001	pbla	24-Mar-01	789-01	6-030	f	adl			18.65	113.00	345	16-May-03	alive		Yes	
2001	pbla	24-Mar-01	790-01	6-041	f	adl	5	A	17.00	117.00	493	07-Apr-04	alive		Yes	Yes
2001	pbla	24-Mar-01	791-01	6-055	f	sb-a	2	A	14.25	106.00	459	26-Jul-03	alive			
2001	pbla	24-Mar-01	792-01	6-116	f	adl	12	A	23.00	127.00	158	11-Nov-01	cnf dead	3614-01	Yes	Yes
2001	pbla	25-Mar-01	796-01	6-067	f	sb-a	2	B	14.85	107.50	480	08-Dec-02	alive			
2001	pbla	25-Mar-01	797-01	6-107	f	adl	10	A	20.75	117.50	4	04-Apr-01	prb dead			
2001	pbla	25-Mar-01	798-01	6-193	m	sb-a	3	B	30.25	130.00	15	02-Jul-01	cnf dead	3544-01	Yes	
2001	pbla	25-Mar-01	799-01	6-132f	f	adl	10	A	17.45	115.00	21	24-May-01	cnf dead	3529-01		
2001	pbla	11-Apr-01	800-01	6-015	f	adl			18.75	118.00	423	13-Sep-02	cnf dead	3784-02		
2001	pbla	12-Apr-01	801-01	6-142	f	adl	12	A	19.45	126.50	47	11-Jul-01	prb dead			
2001	pbla	12-Apr-01	802-01	6-208	f	adl			19.90	118.00	391	24-May-03	alive			
2001	pbla	12-Apr-01	803-01	6-157	f	adl	7	B	16.00	113.50	608	18-Jan-04	cnf dead	4106-04	Yes	Yes
2001	pbla	12-Apr-01	804-01	6-183	m	adl			25.30	123.00	269	12-Mar-04	alive		Yes	Yes
2002	pbla	20-Mar-02	838-02	6-446	f	adl			15.35	115.00	490	16-Sep-03	cnf dead	4003-03	Yes	Yes
2002	pbla	20-Mar-02	839-02	6-458	f	sb-a	3	B	20.90	122.70	539	06-Apr-04	alive		Yes	Yes
2002	pbla	21-Mar-02	840-02	6-495	f	adl	4	B	19.20	111.50	156	27-Aug-02	cnf dead	3776-02	Yes	Yes
2002	pbla	20-Mar-02	841-02	6-522	f	adl	4	B	15.50	117.50	596	21-Mar-03	prb dead			
2002	pbla	21-Mar-02	842-02	6-531	m	adl	4	A	26.30	123.00	237	24-Mar-04	alive		Yes	Yes
2002	pbla	22-Mar-02	843-02	6-544	m	adl	4	A	30.60	26.00	518	07-Apr-04	alive		Yes	Yes
2002	pbla	21-Mar-02	844-02	6-707	f	adl	4	B	15.25	110.20	532	08-Apr-04	alive			
2002	pbla	22-Mar-02	845-02	6-569	f	adl	4	B	15.00	110.30	584	15-Apr-04	alive			
2002	pbla	22-Mar-02	846-02	6-606	f	adl			17.00	115.50	611	18-Apr-04	alive			
2002	pbla	22-Mar-02	847-02	6-622	f	adl	5	A	21.60	117.00	318	21-May-03	cnf dead	3930-03	Yes	Yes
2002	pbla	25-Mar-02	848-02	6-631	m	adl	6	B	25.70	122.90	16	25-Apr-02	cnf dead	3706-02		
2002	pbla	22-Mar-02	849-02	6-647	m	adl	6	B	25.60	124.00	30	15-Aug-02	cnf dead	3769-02	Yes	Yes
2002	pbla	22-Mar-02	850-02	6-655	f	adl	9	A	22.00	119.00	278	18-Apr-04	alive			
2002	pbla	25-Mar-02	851-02	6-672	f	adl			14.50	109.40	648	18-Apr-04	alive			
2002	pbla	25-Mar-02	854-02	6-398	f	adl	6	B	17.30	115.60	619	13-Apr-04	alive			
2002	pbla	21-Mar-02	856-02	6-698	m	juv	1	A	18.40	103.70	33	10-Mar-04	alive			
2002	pbla	08-Oct-02	867-02	6-769	f	sb-a	3	A	16.65	109.00	454	15-Apr-04	alive		Yes	Yes
2002	pbla	08-Oct-02	868-02	6-781	f	adl	7	A	20.65	119.00	364	18-Apr-04	alive		Yes	Yes
2002	pbla	08-Oct-02	870-02	7-555	f	adl	8	B	17.00	110.00	178	23-Mar-04	alive		Yes	
2002	pbla	08-Oct-02	872-02	7-566	f	adl	7	B	17.00	117.00	70	26-Dec-02	cnf dead	3819-02	Yes	Yes
2002	pbla	09-Oct-02	887-02	7-595	f	adl	6	B	19.60	119.00	1407	18-Apr-04	alive		Yes	Yes
2002	pbla	08-Oct-02	888-02	7-604	m	adl	5	B	24.80	123.00	336	18-Apr-04	alive		Yes	Yes
2002	pbla	08-Oct-02	889-02	7-616	m	adl	8	B	22.00	16.00	135	10-Mar-04	alive		Yes	

Table continued

Year	Area	DOC	BRD	Name	Sex	ACL	AYR	AQL	Weight	Length	Resight	Last Seen	Status	Carcass #	TDR	TDR Rec
2002	pbla	09-Oct-02	890-02	7-629	f	adl	4	A	19.80	117.50	484	18-Apr-04	alive		Yes	Yes
2002	pbla	09-Oct-02	891-02	7-642	f	sb-a	3	B	17.70	115.00	408	18-Apr-04	alive		Yes	Yes
2002	pbla	09-Oct-02	892-02	7-654	f	adl	4	B	22.70	120.50	79	05-Jul-03	cnf dead	3966-03	Yes	Yes
2002	pbla	09-Oct-02	893-02	7-664	m	adl	4	A	26.60	126.50	219	18-Apr-04	alive		Yes	Yes
2002	pbla	09-Oct-02	894-02	7-682	m	adl	4	B	23.90	123.00	57	12-Apr-04	cnf dead	4255-04	Yes	Yes
2002	pbla	09-Oct-02	895-02	7-705	f	adl	6	B	19.25	117.00	497	18-Apr-04	alive		Yes	
2002	pbla	09-Oct-02	896-02	7-690	f	adl	5	B	18.95	110.00	226	15-Apr-04	alive		Yes	Yes
2002	pbla	09-Oct-02	897-02	7-717	m	adl	6	B	28.50	128.00	153	09-Mar-04	alive		Yes	Yes
2002	pbla	10-Oct-02	898-02	6-558	F	adl			19.95	120.00	392	18-Apr-04	alive			

* Flipper tag color abbreviations and sex indicators: chartreuse (ch), blue (blue), gold (go), brown (br), white (wh), silver (si), yellow (ye), female (f), and male (m).

** Age estimates were based on cementum analysis of sectioned pre-molar teeth. The AQL code is a reliability index based on the quality of the tooth section, "A" indicates plus or minus 1 year, "B" indicates plus or minus 2 years, and "C" indicates a very poor estimate (error greater than plus/minus 2 years)

*** Status of "cnf dead" indicates confirmed mortality, while "prb dead" indicates likely mortality: animal went missing within 16 months of radio deployment.

Appendix E:

Appendix E. Average move lengths (meters) for each individual sea otter in each study (1980s, Cambria, Monterey Bay) and for each time period (day, week, month, quarter, and year).

Study	Otter	Age	Sex	Day	Week	Month	Quarter	Year
1980	6	a	f	554	1724	2393	2624	*
1980	9	a	f	476	1376	2011	2270	11786
1980	11	a	f	531	1103	1130	1273	1439
1980	14	a	f	963	3638	4887	6944	8942
1980	15	a	f	222	353	370	455	1014
1980	16	a	f	329	1419	2399	3916	3523
1980	19	a	f	324	1321	2038	2866	2885
1980	22	a	f	946	8143	15125	17906	19758
1980	25	a	f	548	1307	2234	3621	8692
1980	27	a	f	781	2485	3319	4084	3571
1980	31	a	f	759	1395	1893	1957	1960
1980	33	a	f	376	924	1518	2305	1183
1980	36	a	f	596	1041	1152	1165	1281
1980	37	a	f	762	1428	3304	4145	*
1980	2	a	m	235	758	*	1857	*
1980	3	a	m	204	557	831	2071	1433
1980	4	a	m	273	506	934	3567	2685
1980	7	a	m	328	598	1008	2606	1873
1980	10	a	m	330	766	1182	14441	1080
1980	17	a	m	437	1096	2387	37684	*
1980	34	a	m	351	5943	23600	*	*
1980	29	s	f	1222	2972	4215	6202	12159
1980	38	s	f	725	*	*	*	*
1980	39	s	f	719	2852	7192	14616	18153
1980	40	s	f	582	1381	2487	5919	29349
1980	42	s	f	376	824	1098	1641	4131
1980	44	s	f	785	1336	*	*	*
1980	45	s	f	587	1455	2052	2653	8691
1980	46	s	f	588	992	1121	1348	1863
1980	47	s	f	1110	1419	2250	3580	4262
1980	13	s	m	629	5440	8459	20040	111525

Appendix E. continued

Study	Otter	Age	Sex	Day	Week	Month	Quarter	Year
1980	30	s	m	1930	5295	9365	16482	72114
1980	35	s	m	1842	4088	6387	7483	7509
1980	41	s	m	1565	3019	4409	4799	7756
1980	43	s	m	1592	2975	5213	9668	5678
Cambria	6-008	a	f	651	1258	1458	1863	1578
Cambria	6-015	a	f	693	1151	2129	2043	1560
Cambria	6-030	a	f	723	1246	3313	4070	2005
Cambria	6-041	a	f	955	2678	1985	2515	6089
Cambria	6-089	a	f	869	1830	*	*	2676
Cambria	6-116	a	f	726	3629	*	*	*
Cambria	6-142	a	f	607	*	1569	1587	*
Cambria	6-157	a	f	670	1174	5555	8848	1749
Cambria	6-208	a	f	1154	3497	2486	3420	5745
Cambria	6-398	a	f	593	1700	1187	1361	2540
Cambria	6-446	a	f	459	823	2300	2846	1006
Cambria	6-458	a	f	882	2149	*	*	2641
Cambria	6-495	a	f	334	876	2907	5024	*
Cambria	6-558	a	f	786	2271	1002	1277	1146
Cambria	6-569	a	f	598	1205	*	*	*
Cambria	6-606	a	f	422	882	2600	3672	1504
Cambria	6-622	a	f	768	1681	4706	3982	5367
Cambria	6-655	a	f	691	2079	907	1080	4671
Cambria	6-672	a	f	461	772	2128	2323	1021
Cambria	6-707	a	f	507	1532	*	19750	2319
Cambria	6-756	a	f	*	*	2503	4866	477
Cambria	6-769	a	f	779	1821	5092	7182	7251
Cambria	6-781	a	f	825	3416	3470	4580	4187
Cambria	7-555	a	f	1138	1877	1089	1784	15384
Cambria	7-566	a	f	408	*	*	*	*
Cambria	7-595	a	f	589	1008	2003	3405	597
Cambria	7-629	a	f	688	1397	6766	15918	4375
Cambria	7-642	a	f	767	2802	*	*	14688
Cambria	7-654	a	f	483	*	2393	2158	*
Cambria	7-690	a	f	904	1874	1498	2131	3535

Appendix E. continued

Study	Otter	Age	Sex	Day	Week	Month	Quarter	Year
Cambria	7-705	a	f	817	1327	*	*	2218
Cambria	6-216	a	m	*	*	21235	64861	117360
Cambria	6-268	a	m	*	*	*	99012	401515
Cambria	6-283	a	m	*	*	10308	233515	85991
Cambria	6-309	a	m	*	*	*	62755	78826
Cambria	6-316	a	m	*	*	22270	82207	42150
Cambria	6-332	a	m	*	*	14587	126754	61945
Cambria	6-342	a	m	*	*	*	53691	1314
Cambria	6-356	a	m	*	*	3923	69982	69564
Cambria	6-371	a	m	*	*	29115	23718	131137
Cambria	6-407	a	m	*	*	*	15904	4683
Cambria	6-421	a	m	*	*	*	31984	*
Cambria	6-433	a	m	*	*	*	80178	3000
Cambria	6-473	a	m	*	*	*	2812	36352
Cambria	6-483	a	m	*	*	*	7559	2539
Cambria	6-531	a	m	447	1471	2582	3433	10680
Cambria	6-631	a	m	182	*	*	*	*
Cambria	6-731	a	m	*	*	*	10367	1983
Cambria	6-647	a	m	149	*	*	*	*
Cambria	7-717	a	m	340	6167	18475	13022	7572
Cambria	6-171	a	m	*	*	870	1252	10190
Cambria	6-183	a	m	471	1683	3021	8707	11578
Cambria	6-226	a	m	*	*	*	3570	115266
Cambria	6-242	a	m	*	*	1634	76115	22788
Cambria	6-259	a	m	309	2256	14918	3599	14600
Cambria	6-298	a	m	*	*	*	21781	27612
Cambria	6-382	a	m	*	*	1859	*	13086
Cambria	6-544	a	m	450	1289	1979	2001	7621
Cambria	7-604	a	m	407	4068	7736	10605	*
Cambria	7-616	a	m	313	1377	18851	29231	*
Cambria	7-664	a	m	290	737	*	36864	*
Cambria	6-055	s	f	257	422	547	606	1551
Cambria	6-067	s	f	285	488	824	1466	518
Cambria	6-522	s	f	369	668	762	946	2580

Appendix E. continued

Study	Otter	Age	Sex	Day	Week	Month	Quarter	Year
Cambria	6-698	s	m	*	*	*	2984	61084
Monterey	193	a	f	440	1485	1323	1802	9931
Monterey	229	a	f	933	*	*	8815	2907
Monterey	230	a	f	656	1302	2730	4333	*
Monterey	257	a	f	325	427	*	*	*
Monterey	4-016	a	f	770	1310	*	*	*
Monterey	4-030	a	f	189	552	*	*	*
Monterey	4-041	a	f	172	1013	1461	1026	*
Monterey	4-058	a	f	380	561	*	*	*
Monterey	4-079	a	f	458	418	*	*	*
Monterey	4-092	a	f	368	557	*	*	1757
Monterey	4-156	a	f	426	727	916	1515	2947
Monterey	4-168	a	f	*	*	1017	2947	260
Monterey	4-191	a	f	256	714	*	*	*
Monterey	4-244	a	f	370	663	*	*	*
Monterey	4-257	a	f	177	479	*	*	1314
Monterey	4-302	a	f	228	1097	2103	6191	8383
Monterey	4-538	a	f	352	505	641	857	1179
Monterey	4-587	a	f	412	1048	1471	1813	673
Monterey	4-596	a	f	540	654	2606	3609	2360
Monterey	4-643	a	f	*	*	650	872	1753
Monterey	4-883	a	f	330	553	1251	1150	1420
Monterey	4-896	a	f	242	910	2032	2619	1683
Monterey	4-944	a	f	667	1524	5383	5767	2895
Monterey	5-102	a	f	425	1893	2617	2920	4744
Monterey	5-374	a	f	521	926	536	871	445
Monterey	5-421	a	f	127	228	1938	1996	1951
Monterey	5-441	a	f	255	1083	2510	4800	1267
Monterey	5-550	a	f	320	804	2906	3702	6311
Monterey	5-578	a	f	329	1594	3329	10281	7918
Monterey	5-633	a	f	453	1830	2713	8040	30822
Monterey	5-672	a	f	386	1791	5732	5194	*
Monterey	5-705	a	f	602	1517	2776	4931	4228
Monterey	5-928	a	f	369	1127	2053	2759	6008

Appendix E. continued

Study	Otter	Age	Sex	Day	Week	Month	Quarter	Year
Monterey	5-936	a	f	428	1186	985	961	*
Monterey	5-952	a	f	240	336	*	*	2872
Monterey	6-723	a	f	268	599	*	4268	2296
Monterey	732-99	a	f	*	*	1108	1019	1217
Monterey	899-03	a	f	461	469	*	5311	2231
Monterey	7-682	a	m	*	*	*	54448	*
Monterey	4-204	a	m	215	572	1648	3121	8849
Monterey	4-441	a	m	*	*	*	1900	3054
Monterey	4-612	a	m	157	422	1135	836	873
Monterey	4-747	a	m	260	289	579	838	2162
Monterey	4-761	a	m	199	339	529	1863	4508
Monterey	4-904	a	m	170	314	842	5302	8598
Monterey	5-148	a	m	321	635	1879	12128	588
Monterey	5-739	a	m	174	*	*	*	6636
Monterey	5-861	a	m	900	919	3053	2204	3053
Monterey	5-993	a	m	233	486	1670	3331	2450
Monterey	743-99	a	m	195	474	2073	755	1715
Monterey	886-02	a	m	250	405	551	1361	*
Monterey	6-569	s	f	*	*	1500	1709	1877
Monterey	Jillian	s	f	*	858	1799	557	2157
Monterey	198-01	s	f	470	717	1155	2040	57699
Monterey	Blue	s	m	*	*	*	17641	416
Monterey	Frankie	s	m	*	*	*	2779	489921
Monterey	Max	s	m	*	296	649	721	*
Monterey	Moose	s	m	*	*	*	5085	*

Appendix F:

Appendix F. Home range calculations using four methods; minimum convex polygon (MCP), adaptive kernel (AK), adjusted kernel (ADJK), and calculated area of use (CAU). Areas (m^2) are calculated for each individual sea otter within three studies; 1980s, current Cambria (Cam), and the current Monterey Bay sub-population.

Study	Otter	Class	MCP	AK	ADJK	Lin	Offshore	CUA	N
1980s	9	af	44	32.4	19.1	5	1.5	7.5	380
1980s	11	af	20	3.5	3.5	5	2.5	12.5	437
1980s	14	af	71	55.0	32.0	20.5	0.65	13.3	539
1980s	15	af	7	0.4	0.4	1.5	0.55	0.8	490
1980s	16	af	46	15.9	12.3	21	0.9	18.9	397
1980s	19	af	25	7.2	5.8	6.5	0.7	4.6	352
1980s	22	af	468	237.2	133.7	51.5	1.25	64.4	343
1980s	25	af	71	23.0	14.8	15	0.6	9.0	401
1980s	27	af	42	20.3	14.1	11.5	0.6	6.9	273
1980s	31	af	13	6.6	5.1	8	0.6	4.8	448
1980s	33	af	19	10.1	6.9	10.5	0.5	5.3	430
1980s	36	af	17	2.5	2.0	4.5	0.85	3.8	512
1980s	29	sf	111	101.5	70.3	27	1.65	44.6	360
1980s	39	sf	485	185.6	102.1	30	1.25	37.5	341
1980s	40	sf	646	509.4	310.1	42	1.35	56.7	432
1980s	42	sf	43	5.7	4.4	5	1.05	5.3	467
1980s	45	sf	149	20.9	14.6	8	1.05	8.4	272
1980s	46	sf	38	7.0	6.4	5.25	1.7	8.9	522
1980s	47	sf	40	13.7	12.0	11.5	1.25	14.4	234
1980s	13	sm	2139	2124.2	1059.7	133	2.7	359.1	225
1980s	30	sm	2497	1112.0	644.6	85.5	2.7	230.9	373
1980s	35	sm	232	95.6	74.2	22	2.9	63.8	345
1980s	41	sm	189	57.0	54.0	16.5	3.05	50.3	329
1980s	43	sm	553	282.0	202.9	36.5	3	109.5	341
1980s	3	am	78	9.4	6.2	5	0.7	3.5	277
1980s	4	am	155	16.0	11.0	4.5	0.75	3.4	230
1980s	7	am	104	48.3	30.6	14	1.05	14.7	476
1980s	10	am	661	35.4	19.9	8	1.25	10.0	444
1980s	17	am	458	126.9	72.1	20	1	20.0	220
1980s	34	am	1414	1523.4	745.6	74	1.8	133.2	110
Cam	6-008	af	7	4.6	4.2	6	1	6.0	500
Cam	6-015	af	9	3.9	3.7	4	1.5	6.0	380

Appendix F. continued

Study	Otter	Age	MCP	Kernel	ADJK	Lin	Offshore	CUA	N
Cam	6-030	af	41	15.1	12.0	10	2	20.0	140
Cam	6-041	af	26	30.8	22.7	16	1	16.0	408
Cam	6-089	af	35	11.9	10.2	8.5	1.2	10.2	490
Cam	6-116	af	58	73.4	49.2	24	1.25	30.0	140
Cam	6-157	af	33	4.8	4.3	4.25	0.7	3.0	580
Cam	6-208	af	140	77.7	47.8	21.5	1.25	26.9	340
Cam	6-398	af	24	15.7	12.9	12.5	1	12.5	432
Cam	6-446	af	19	2.0	2.0	3	1.25	3.8	460
Cam	6-458	af	17	10.6	10.1	8.5	1.1	9.4	397
Cam	6-495	af	4	1.4	1.1	2	0.5	1.0	144
Cam	6-558	af	10	9.1	7.1	7.25	0.75	5.4	220
Cam	6-606	af	11	2.5	2.4	4.5	0.75	3.4	435
Cam	6-622	af	64	11.4	9.9	8	1	8.0	308
Cam	6-655	af	54	21.3	15.2	12	1	12.0	66
Cam	6-672	af	17	2.6	2.5	4	1	4.0	452
Cam	6-707	af	27	4.6	4.1	5	0.8	4.0	383
Cam	6-769	af	22	14.7	12.3	9	1	9.0	248
Cam	6-781	af	84	44.3	30.8	15.5	1	15.5	208
Cam	7-555	af	63	80.4	55.1	26.5	1.25	33.1	118
Cam	7-595	af	14	4.6	3.8	4.5	0.75	3.4	250
Cam	7-629	af	25	8.1	7.2	7.5	0.75	5.6	296
Cam	7-642	af	128	165.6	88.4	28.5	0.75	21.4	244
Cam	7-690	af	12	13.5	11.9	9	1	9.0	142
Cam	7-705	af	15	12.8	10.8	8.5	1	8.5	303
Cam	6-569	sf	14	7.4	6.8	7	1.25	8.8	388
Cam	6-055	sf	5	0.9	0.9	2	1	2.0	423
Cam	6-067	sf	29	2.9	2.3	2.5	0.75	1.9	375
Cam	6-522	sf	12	1.6	1.6	3	1	3.0	277
Cam	6-698	sm	353	1252.3	690.2	79	2	158.0	51
Cam	6-171	am	338	180.7	82.0	18.5	1.25	23.1	56
Cam	6-183	am	283	48.5	29.2	10.5	1	10.5	238
Cam	6-259	am	2223	735.7	334.9	43	1	43.0	275
Cam	6-382	am	708	1169.5	585.1	68	1.5	102.0	54
Cam	6-531	am	638	107.4	58.9	13	1.25	16.3	159
Cam	6-544	am	152	16.6	10.8	5	1	5.0	217

Appendix F. continued

Study	Otter	Age	MCP	Kernel	ADJK	Lin	Offshore	CUA	N
Cam	7-717	am	606	580.8	308.5	31	1	23.3	101
Cam	7-604	am	102	102.2	55.6	16	0.75	12.0	161
Cam	7-616	am	2253	544.0	252.5	31.5	1.25	39.4	97
Cam	7-664	af	446	129.7	76.2	16	1	16.0	117
MBA	193	af	2	2.1	1.6	3.5	0.25	0.9	95
MBA	230	af	24	18.5	12.8	13	1	13.0	201
MBA	4-156	af	3	1.3	1.2	3.5	0.5	1.8	113
MBA	4-168	af	10	3.6	2.8	4.5	0.5	2.3	352
MBA	4-302	af	4	1.6	1.2	3.5	0.25	0.9	309
MBA	4-538	af	43	5.2	4.1	7	0.5	3.5	166
MBA	4-587	af	7	1.5	1.2	4	0.25	1.0	193
MBA	4-596	af	8	2.3	1.9	5	0.25	1.3	350
MBA	4-643	af	10	6.3	4.9	7	0.5	3.5	56
MBA	4-883	af	38	0.9	0.8	2.5	0.25	0.6	416
MBA	4-896	af	6	2.3	1.8	3	0.5	1.5	108
MBA	4-944	af	19	6.7	4.7	7.5	0.5	3.8	343
MBA	5-102	af	84	13.4	8.0	9	0.5	4.5	157
MBA	5-374	af	29	4.0	3.0	5.5	0.25	1.4	257
MBA	5-421	af	6	0.9	0.5	1.5	0.25	0.4	54
MBA	5-441	af	73	2.8	2.1	4	0.5	2.0	193
MBA	5-550	af	84	5.3	3.9	5.5	0.5	2.8	321
MBA	5-578	af	20	13.8	10.2	10.5	0.75	7.9	183
MBA	5-633	af	71	20.0	12.4	11	0.25	2.8	110
MBA	5-672	af	109	40.1	27.8	16.5	0.5	8.3	71
MBA	5-705	af	51	25.6	16.2	19	0.25	4.8	149
MBA	5-928	af	39	7.3	5.4	8.5	0.25	2.1	215
MBA	5-936	af	23	3.9	2.9	5.5	0.25	1.4	252
MBA	6-723	af	10	3.6	2.8	5.5	0.5	2.8	350
MBA	899	af	3	1.3	1.1	3.5	0.5	1.8	123
MBA	Jillian	sf	15	15.2	10.7	8	0.5	4.0	57
MBA	198	sf	5	1.1	1.0	3	0.25	0.8	250
MBA	Max	sm	2	2.6	2.4	4.25	1	4.3	54
MBA	4-204	am	61	0.5	0.4	1	0.5	0.5	436
MBA	4-612	am	16	0.2	0.2	1	0.5	0.5	309
MBA	4-747	am	17	0.5	0.4	1.5	0.5	0.8	121

Appendix F. continued

Study	Otter	Age	MCP	Kernel	ADJK	Lin	Offshore	CUA	N
MBA	4-761	am	7	0.5	0.3	1.75	0.5	0.9	172
MBA	4-904	am	24	1.1	0.8	1.5	1.25	1.9	186
MBA	5-148	am	39	1.9	1.2	2	1	2.0	205
MBA	5-861	am	22	11.5	9.9	5.5	1.5	8.3	54
MBA	5-993	am	62	0.6	0.5	1	0.9	0.9	419
MBA	743	am	61	0.6	0.5	2	1	2.0	425
MBA	886	am	17	0.5	0.4	1	0.5	0.5	130
MBA	421	am	13	0.7	0.5	1.25	0.5	0.6	130

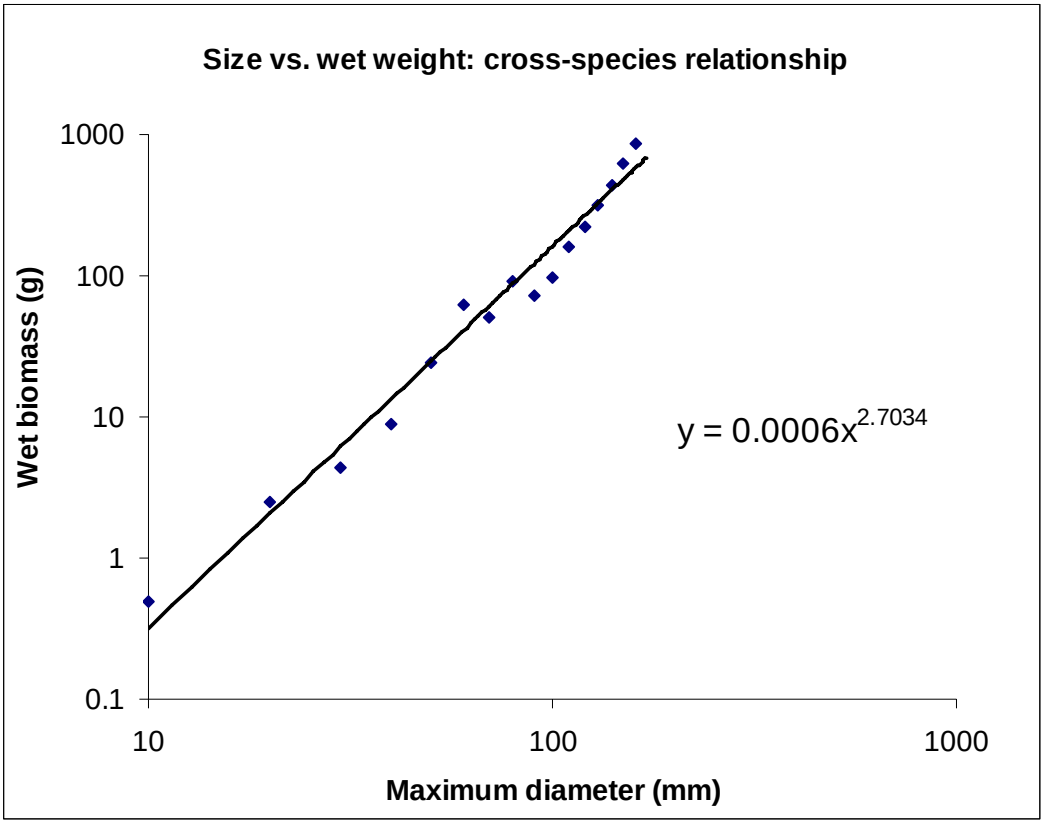
Appendix G:

Prey biomass and energy content conversion parameters used for analyses of diet content (by weight) and rate of energy acquisition. Referenced literature is cited as numbers in tables: full citations are provided at bottom.

i) Prey diameter (mm) to wet edible biomass (g) conversion equations from the published literature for 7 species, and generalized cross-species function used to convert remaining species (calculated as the average, best-fit relationship for the 7 known species across their appropriate size ranges: see graph).

Species used to derive generalized, cross-species relationship

Prey species	Equation	Parameter a	Parameter b	Reference
washington clam	a*size^b	0.0001	2.5550	2
purple urchin	exp(a+b*size)	-1.6077	0.0907	1
red abalone	exp(a+b*size)	2.3070	0.0224	1
turban snail	exp(a+b*size)	-3.0770	0.1419	1
ochre star	exp(a+b*size)	0.2500	0.0436	1
rock crab	exp(a+b*size)	1.9143	0.0340	1
kelp crab	exp(a+b*size)	1.6327	0.0142	1
Generalized relationship:	**a*size^b**	**0.0006**	**2.7034**	(see graph)



ii) Mean recorded size (in cm) for each prey type and the associated estimated wet edible biomass (calculated using above equations).

				Energy Content (kJ per item)			
Prey Type	References	Mean Size (cm)	Mean estimated wet biomass (g)	Size 1 (1-5 cm)	Size 2 (6-10 cm)	Size 3 (11-15 cm)	Size 4 (>15 cm)
kelp crab	1,4	3.9	10	19.9	40.4	65.4	-
turban snail	4	2.5	3	25.3	-	-	-
mussel	3,4,7	3.4	9	2.5	37.4	-	-
purple urchin	1	4	8	5.6	104.6	-	-
clam, unidentified species	8	4.3	16 [2]	8.6	99.1	394.0	-
cancer crab	1,4	9.3	160	47.8	261.3	1428.1	2183.9
crab, unidentified species	8	4.1	15 [2]	33.8	150.8	1307.6	2183.9
fat innkeeper worm	6	6.3	22	25.5	51.4	51.4	-
Small kelp fuana		N/A	10 [1]		(15)		
sea star	8	6.6	23	5.5	35.8	42.6	-
sand crab		2.7	5 [2]	10.0	-	-	-
sand dollar		3.5	9 [2]	5.0	-	-	-
abalone	1	13.9	226	8.4	229.9	704.2	3637.8
octopus	5	7.6	67	13.5	208.6	870.8	3291.8
worm, unknown species	8	5.9	10 [1]	12.7	25.7	25.7	-
chiton	4	4.5	19 [2]	6.7	100.5	279.1	-
limpet	8	2.4	4 [2]	6.7	49.8	-	-
scallop	1,3,6	8	73	8.0	85.1	-	-
cockle	2,8	10	162 [2]	8.1	97.2	247.7	-
gaper clam	1,3,6	7	59	9.1	107.3	382.8	-
sea cucumber	8	3.8	12 [2]	7.5	20.0	25.0	-
red urchin	1	4.3	12	14.1	142.8	571.5	-
Squid	1	4.3	16 [2]	6.8	104.3	435.4	1645.9
isopod	8	2.4	4 [2]	10.0	-	-	-

[1] Not derived from equations because size was impossible to measure. Value represents approximation based on average handling times.
[2] Size-biomass conversion calculations used generalized, cross-species relationship (see above)

iii) Literature used for size-biomass and biomass-energy conversion parameters:

1. Costa, D. P. 1978. The ecological energetics, water, and electrolyte balance of the California sea otter (*Enhydra lutris*). Ph.D. dissertation. University of California, Santa Cruz, Santa Cruz, CA.

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3. Ebert, E. E. 1968. A food habits study of the southern sea otter, Enhydra lutris nereis. California Fish and Game **54**:33-42.

4. Faurot, E. R., J. A. Ames, and D. P. Costa. 1986. Analysis of sea otter, Enhydra lutris, scats collected from a California haulout site. Mar. Mammal Sci. **2**:223-227.

5. Hernández-López, J. L., J. J. Castro-Hernández, and H.-G. Vicente. 2001. Age determined from the daily deposition of concentric rings on common octopus (*Octopus vulgaris*) beaks. Fisheries Bulletin **99**:679–684.

6. Jolly, J. M. 1997. Foraging ecology of the sea otter, *Enhydra lutris*, in a soft-sediment community. Masters dissertation. University of California, Santa Cruz, Santa Cruz, CA.

7. Mathews, C. R. 1996. Diet Profitability for the California Sea Otter, *Enhydra lutris*. Masters dissertation. University of California, Santa Cruz, Santa Cruz, CA.

8. Wacasey, J. W., and E. G. Atkinson. 1987. Energy values of marine benthic invertebrates from the Canadian Arctic. Marine Ecology Progress Series **39**:243-250.

Appendix H:

Summary of Discriminant Analysis Results

		Standardized Canonimal Coefficients		
Prey Type	F-to-Remove	Factor 1	Factor 2	Total (absolute)
snail	42.49	0.191	0.947	1.138
cancer crab	10.62	-0.822	0.174	0.996
clam	9.34	0.724	-0.446	1.17
worm	4.07	0.337	-0.398	0.735
abalone	2.58	-0.432	0.139	0.571
mussel	2.28	0.248	-0.355	0.603
other (sand)	2.07	0.079	-0.486	0.565
sea star	1.6	-0.478	0.074	0.552
crab (un-id)	1.53	-0.351	0.034	0.385
kelp crab	1.43	0.183	-0.291	0.474
urchin	1.42	0.127	-0.294	0.421
other (rock)	0.43	0.006	-0.164	0.17
cephalapod	0.09	-0.054	-0.053	0.107

Group Means	Cluster 1	Cluster 2	Cluster 3
abalone	5.125	1.155	0.259
clam	1.453	4.502	0.710
cancer crab	22.376	7.393	0.975
cephalapod	0.813	0.456	0.048
crab (un-id)	0.977	0.572	0.246
kelp crab	1.636	0.939	0.669
mussel	0.670	2.105	0.175
other (sand)	0.004	0.881	0.000
other (rock)	0.259	0.569	0.008
snail	0.361	0.170	9.353
sea star	0.826	0.129	0.401
urchin	1.499	1.664	0.531
worm	0.238	2.595	0.085

Diagnostic Statistics

Wilks' lambda= 0.050
Approx.F= 12.031 df= 26, 90 p-tail= 0.0000

Pillai's trace= 1.545
Approx.F= 12.015 df= 26, 92 p-tail= 0.0000

Lawley-Hotelling trace= 7.114
Approx.F= 12.039 df= 26, 88 p-tail= 0.0000

	Cluster 1	Cluster 2	Cluster 3
Group Frequencies:	20	34	6

Classification matrix (cases in row categories classified into columns)

	Cluster 1	Cluster 2	Cluster 3	%correct
1	1	33	0	97
2	19	0	1	95
3	0	0	6	100
Total:	**20**	**33**	**7**	**97**

Jackknifed classification matrix

	Cluster 1	Cluster 2	Cluster 3	%correct
1	2	32	0	94
2	19	0	1	95
3	0	1	5	83
Total	**21**	**33**	**6**	**93**

Factor Eigenvalues:	4.414	2.699
Canonical correlations:	0.903	0.854
Cumulative proportion of total dispersion:	0.621	1

Appendix I:

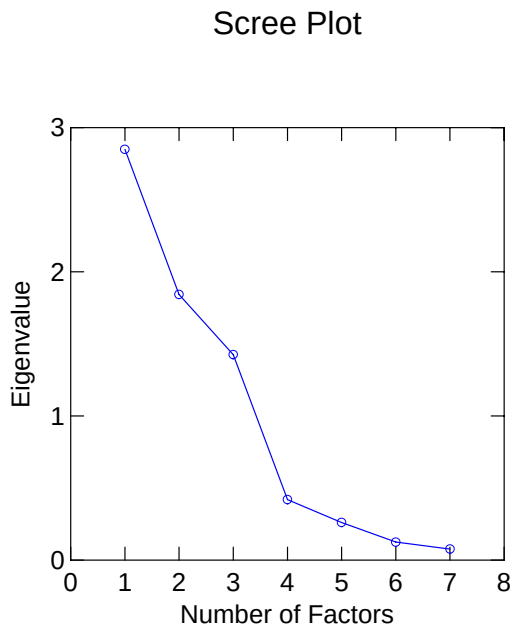
Summary of Principal Component Analysis Results

Latent Roots (Eigenvalues):

1	2	3	4	5	6	7
2.848	1.843	1.426	0.420	0.261	0.125	0.077

Percent of Total Variance Explained by First 3 Components:

1	2	3
40.690	26.325	20.365



Component loadings:

	1	2	3
Handling time/item	-0.939	-0.051	-0.082
Variance in ST	-0.892	0.303	-0.112
Mean ST	-0.671	0.660	0.244
Dive success rate	0.620	0.406	0.531
Number items/dive	0.453	0.803	0.026
SDR	0.080	0.709	-0.540
Dive duration	-0.353	0.018	0.879

Coefficients for Standardized Factor Scores

	1	2	3
Handling time/item	-0.330	-0.027	-0.057
Variance in ST	-0.313	0.165	-0.078
Mean ST	-0.236	0.358	0.171
Dive success rate	0.218	0.220	0.372
Number items/dive	0.159	0.436	0.018
SDR	0.028	0.385	-0.379
Dive duration	-0.124	0.010	0.617

The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The MMS **Royalty Management Program** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principles of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.