

UNIVERSITY OF CALIFORNIA

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**SOURCES OF VARIATION IN THE FORAGING BEHAVIOR
AND DEMOGRAPHY OF THE SEA OTTER, *ENHYDRA LUTRIS***

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**SOURCES OF VARIATION IN THE FORAGING BEHAVIOR
AND DEMOGRAPHY OF THE SEA OTTER, *ENHYDRA LUTRIS***

Martin Tim Tinker

Abstract

I investigated demography and foraging behavior of the southern sea otter (*Enhydra lutris nereis*), in order to examine the individual and population-level consequences of alternative foraging strategies, and to evaluate the importance of food-limitation as a factor limiting population growth. I developed a maximum likelihood-based analytical method to estimate historical age/sex-specific vital rates, and spatial/temporal variation in vital rates, using carcass age-structure and population census databases. To estimate current demographic trends I conducted a mark-recapture study, measuring survival and reproduction of 115 radio-tagged study animals between 2001 and 2004. Together, these analyses indicate that survival has decreased substantially between the early 1990s and the present, and is lowest in the north-central portion of the sea otter's range. The greatest decrease was for adult (> 4 years of age) females: variation in survival of this age/sex class is primarily responsible for regulating population growth and driving population trends.

I also collected foraging data from 60 marked sea otters, and found pronounced individual dietary specialization (greater than that reported previously). Cluster analysis indicated that individual diets could be grouped into three general "diet types"; differences in foraging behavior between these diet types suggest that they represent distinct foraging strategies. The rate of energy gain while foraging was low for the population as a whole, but showed a high degree of variation. Foraging strategies differed with respect to mean energy gain; however, because the mean and within-animal variation in rate of energy gain were

positively correlated, all three strategies result in similar probabilities of exceeding a critical rate of energy gain on any given day, and there is likely a trade-off between the mean and variance in the rate of energy gain. Correlational selection is also important in maintaining multiple foraging strategies within the population: a multivariate fitness surface fit to foraging behavior indicates multiple fitness peaks corresponding to alternative foraging strategies. I suggest that food-limitation is likely an important ultimate factor restricting population growth in the center of the sea otters' range in California, but that the existence of alternative foraging strategies may obscure expected patterns of density dependence.

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Introduction

The southern sea otter (*Enhydra lutris nereis*) narrowly escaped extinction at the beginning of the 20th century, primarily as a result of the international fur trade (Kenyon 1969). After receiving protection from hunting pressure, however, the population recovered from a tiny remnant colony of approximately 100 animals in 1938 (located along the Big Sur coastline near Bixby creek) to a population of over 2500 individuals by 1994, ranging between Half Moon Bay in the north to Pt. Conception in the south (Kenyon 1969, Estes et al. 2003a). Throughout this period the rate of recovery was sluggish compared to other recovering or translocated populations (Estes 1990), and the population remains listed as threatened under the Endangered Species Act (USFWS 2003). Between 1994 to 1999 the population actually underwent a significant decline (Estes et al. 2003a); although population recovery now appears to have resumed (based on more recent range-wide population counts: USGS, unpublished data), the cause(s) of the 1990's decline remain uncertain, as does the relative importance of prey abundance as a factor potentially limiting future population growth in portions of the range.

The relative abundance of prey resources has been found to be the factor ultimately limiting population growth in sea otter populations in Alaska and Russia (Garshelis et al. 1986, Estes 1990, Estes et al. 1996, Bodkin et al. 2000). For these northern populations, as with many other apex predators, it appears that carrying capacity is reached when the abundance of one or more important prey populations (e.g. green sea urchins, *Strongylocentrotus droebachiensis*) becomes sufficiently reduced by predation pressure (Estes and Duggins 1995). Because predation pressure increases as a function of sea otter density, individual foraging success therefore tends to be negatively density-dependant

(Estes et al. 1981, Estes et al. 1982, Dean et al. 2002). Although these patterns appear to be relatively consistent across most northern populations, the situation is somewhat less clear for the southern sea otter. There is strong evidence that the periods of population decline in California are associated with increased mortality rather than decreased reproduction (Estes et al. 2003a), and much attention has been focused on the role of infectious diseases as a primary source of this mortality (e.g. Thomas and Cole 1996, Miller et al. 2002, Kreuder et al. 2003). Evidence for the importance of infectious disease derives from detailed examination of fresh beach-cast carcasses, which are collected throughout the sea otters range in California as part of a long-term and comprehensive inter-agency salvage program (Ames et al. 1983, Estes et al. 2003a). In addition to infectious disease, analysis of the carcass database indicates myriad other sources of mortality in the southern sea otter, including direct human-caused mortality (e.g. boat strikes, shooting), shark bite, entanglement in fishing gear, naturally-occurring or anthropogenic toxins, mating trauma (or other injuries inflicted by con-specifics), and emaciation (Estes et al. 2003a).

Since 1992 there have been relatively few fresh carcasses for which emaciation has been determined to be the primary cause of death (Kreuder et al. 2003), and in view of this fact there has been little consideration of density-dependant food limitation as a factor limiting recovery of the southern sea otter. However, there are a number of reasons why food limitation should not be dismissed as an important factor in this population. First, the fact that prey resources are the chief determinants of carrying capacity in other sea otter populations is by itself sufficient reason to include food limitation as one of several potential hypotheses about the sources of population regulation in the southern sea otter. Second, it is overly simplistic to expect that food limitation would be evident solely as an increase in the

number of otters dieing from starvation: in fact, one of the chief manifestations of energetic or nutritional stress is an increase in disease, resulting from compromised immune function (Cunningham-Rundles 2002). Thus a high level of disease-related mortality is not by itself inconsistent with a hypothesis of food limitation as an ultimate causal factor, because food-stress could be underlying other proximate causes of death. Third, the precise demographic impacts of food limitation in the southern sea otter are difficult to predict due to the varied diet (Ostfeld 1982) and high degree of individual dietary specialization (Estes et al. 2003b). Estes et al. (2003b) showed that individual otters inhabiting the same geographic locations may have almost non-overlapping diets, which means that any nutritional deficiencies caused by reductions of particular prey populations would likely impact certain individuals but not others, resulting in complex and variable effects of food limitation on demography. Detecting food limitation in the southern sea otter may therefore be less straightforward than in Alaskan populations: a first step in resolving this issue will be to clarify the specific patterns of demographic change that are responsible for the observed fluctuations in population growth.

Sea otters have an extraordinarily high mass-specific metabolic rate (Costa 1978), primarily as a consequence of high thermoregulatory demands created by their small size (and thus high surface-to-volume ratio as compared to most other marine mammals) and lack of blubber insulation (Costa and Kooyman 1982). The high energetic requirements of sea otters, in conjunction with their inability to store significant quantities of energy as fat reserves and the fact that individual foraging success is density-dependant, would lead us to expect that foraging behavior and diet selection must be under particularly intense selection pressure in this species. This feature, in conjunction with their tractability as a study animal

(they handle and consume all prey at the surface and usually within sight of the shore where they can be readily observed) makes them an ideal candidate for studies of foraging behavior.

Sea otters are particularly suitable for testing optimality models, which often assume that energy-maximizing decisions are equivalent to fitness-maximizing decisions (Stephens and Krebs 1986); in sea otters this assumption may actually be warranted because their survival and reproductive success depends on maintaining a high rate of energy input (Monson et al. 2000). Given this fact, it is therefore somewhat surprising that different individuals have such unique diets (Estes et al. 2003b), each of which likely has different energetic consequences (Mathews 1996). One might instead expect selection to push foraging behavior towards a single “optimal” strategy. Estes et al. (2003b) speculated that individuals probably specialize because the foraging skills required for different prey types are highly divergent and difficult to learn, and thus specialists have greater foraging efficiency than generalists: this, in conjunction with cultural transmission of foraging skills from mothers to pups and frequency-dependent dynamics, could act to maintain alternative specializations in the population. This phenomenon certainly requires further investigation, both in terms of better understanding the mechanisms that maintain alternative specializations and in terms of resolving the implications for individual fitness (and, ultimately, for demography and population dynamics).

The research that is summarized in the following chapters was designed to address three broad objectives, which may seem at first glance to be somewhat disparate but are in fact highly interrelated. First, I set out to describe spatial/temporal variation in the demography of the southern sea otter, and in particular to determine the specific changes that

were responsible for population decline during 1990s. This first objective was achieved by analyzing a variety of historical data sources, and combining the results with a mark-recapture analysis of data collected from an ongoing, telemetry-based study of the current population: this work is presented in chapter 1. Second, I wished to study in more depth the patterns of variation in diet and foraging behavior in this population, to determine a) whether individual dietary specialization corresponds to readily distinguishable foraging strategies, and b) the implications of alternative foraging strategies for individual fitness, for foraging success in general, and ultimately for population dynamics. To achieve this objective I studied foraging behavior in a sample of marked study animals at two study sites over a three year period: the results of this work are presented in chapter 2. Finally, I sought to better understand the mechanisms that lead to coexistence of alternative specializations in this population, or indeed any population, and in particular to examine the potential roles of learned foraging skills and cultural transmission. To achieve this last objective using empirical data collected from sea otters turned out to be beyond the scope of a single graduate career; however, as a first step in attacking this problem I developed a series of dynamic, quantitative models that together explore the interactive effects of learning behavior, cultural transmission and frequency-dependent foraging success on the prevalence of alternative foraging specializations in a population. These models are presented in chapter 3.

References

- Ames, J. A., R. A. Hardy, F. E. Wendell, and J. J. Geibel. 1983. Sea otter mortality in California. Marine Resources Branch, California Fish and Game.
- Bodkin, J. L., A. M. Burdin, and D. A. Ryazanov. 2000. Age- and sex-specific mortality and population structure in sea otters. *Marine Mammal Science* **16**:201-219.
- 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.
- Costa, D. P., and G. L. Kooyman. 1982. Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. *Canadian Journal of Zoology* **60**:2761-2767.
- Cunningham-Rundles, S. 2002. Evaluation of the effects of nutrients on immune function. Pages 21-39 in P. C. Calder, C. J. Field, and H. S. Gill, editors. *Nutrition and Immune Function*. CABI Publishing, Wallingford, UK.
- Dean, T. A., J. L. Bodkin, A. K. Fukuyama, S. C. Jewett, D. H. Monson, C. E. O'Clair, and G. R. VanBlaricom. 2002. Food limitation and the recovery of sea otters following the 'Exxon Valdez' oil spill. *Marine Ecology-Progress Series* **241**:255-270.
- Estes, J. A. 1990. Growth and equilibrium in sea otter populations. *Journal of Animal Ecology* **59**:385-402.
- Estes, J. A., D. F. Doak, J. R. Bodkin, R. J. Jameson, D. H. Monson, J. Watt, and M. T. Tinker. 1996. Comparative demography of sea otter populations. *Endangered Species Update* **13**:11-13.
- Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: Generality and Variation in a Community Ecological Paradigm. *Ecological Monographs* **65**:75-100.
- Estes, J. A., B. B. Hatfield, K. Ralls, and J. Ames. 2003a. Causes of mortality in California sea otters during periods of population growth and decline. *Marine Mammal Science* **19**:198-216.
- Estes, J. A., R. J. Jameson, and A. M. Johnson. 1981. Food selection and some foraging tactics of sea otters. Pages 606-641 in J. A. Chapman and D. Pursley, editors. *Worldwide Furbearer Conference Proceedings, Volume 1*. University of Maryland Press, Baltimore, Maryland.
- Estes, J. A., R. J. Jameson, and E. B. Rhode. 1982. Activity and prey selection in the sea otter: influence of population status on community structure. *American Naturalist* **120**:242-258.

- Estes, J. A., M. L. Riedman, M. M. Staedler, M. T. Tinker, and B. E. Lyon. 2003b. Individual variation in prey selection by sea otters: patterns, causes and implications. *Journal of Animal Ecology* **72**:144-155.
- Garshelis, D. L., J. A. Garshellis, and A. T. Kimker. 1986. Sea otter time budgets and prey relationships in Alaska. *Journal of Wildlife Management* **50**:637-647.
- Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. *North American Fauna* **68**:1-352.
- Kreuder, C., M. A. Miller, D. A. Jessup, L. J. Lowenstine, M. D. Harris, J. A. Ames, T. E. Carpenter, P. A. Conrad, and J. A. K. Mazet. 2003. Patterns of mortality in southern sea otters (*Enhydra lutris nereis*) from 1998-2001. *Journal of Wildlife Diseases* **39**:495-509.
- Mathews, C. R. 1996. Diet Profitability for the California Sea Otter, *Enhydra lutris*. Masters dissertation. University of California, Santa Cruz, Santa Cruz, CA.
- Miller, M. A., I. A. Gardner, C. Kreuder, D. M. Paradies, K. R. Worcester, D. A. Jessup, E. Dodd, M. D. Harris, J. A. Ames, A. E. Packham, and P. A. Conrad. 2002. Coastal freshwater runoff is a risk factor for *Toxoplasma gondii* infection of southern sea otters (*Enhydra lutris nereis*). *International Journal for Parasitology* **32**:997-1006.
- Monson, D. H., J. A. Estes, J. L. Bodkin, and D. B. Siniff. 2000. Life history plasticity and population regulation in sea otters. *Oikos* **90**:457-468.
- Ostfeld, R. S. 1982. Foraging strategies and prey switching in the California sea otter. *Oecologia* **53**:170-178.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ.
- Thomas, N. J., and R. A. Cole. 1996. The risk of disease and threats to the wild population. *Endangered Species Update* **13**:23-27.
- USFWS. 2003. Final revised recovery plan for the southern sea otter (*Enhydra lutris nereis*). U.S. Fish and Wildlife Service. Portland, OR.

Chapter 1. Spatial and temporal variation in the demography of southern sea otters

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 southern 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 I develop a methodological approach to inferring patterns of demographic variation in a population. In part 1, I 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, I apply this method to the 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 1.1), it is less clear what specific demographic changes were responsible for the change in population dynamics. 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: I 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 I 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 I used 11 spring counts made during the period 1992–2002: the numbers counted during these surveys ranged from 1790 to 2095. For dependent pups I 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, I 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. I 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

My 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 dieing 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. I 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), I formulated the model in terms of discrete age classes, with the time-step set to 1 year. This simplifies presentation of results, and better corresponds to the discrete 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). I 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:

$$S_{x,y,t,g} = \frac{e^{f_x+f_y+f_t+f_g}}{1 + e^{f_x+f_y+f_t+f_g}} \quad 1$$

where f_x, f_y, f_t, f_g are sub-functions that specify the effects of age, sex, time and location, respectively. I conducted all calculations for animals aged 1 year or greater ($x = 1, 2 \dots 19$ years old): for the first year class, $x = 0$, I set survival probabilities equal to that of 1 year olds ($x = 1$). While this is likely a reasonable approximation (Monson et al. 2000a), I have no way to directly gauge its validity because I 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:

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

where $[\theta_1 \theta_2 \theta_3 \theta_4]$ 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 my 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), I 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).

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

$$f_y = y \cdot \theta_5 + x \cdot y \cdot \theta_6 \quad 3$$

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, I 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, I modeled changes in survival that could be gradual or rapid, but were still continuous across years:

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

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, I also considered changes in survival that may have occurred suddenly, effectively treating time as a categorical variable:

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

where A is a switch variable: $A = 0$ if $t < \theta_i$, $A = 1$ if $t \geq \theta_i$, and θ_i 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), I also fit models allowing for three or four time categories.

I incorporated spatial variation in survival by defining discrete geographic areas: specifically, I 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, I first divided the current range of the southern sea otter into 10 contiguous coastline segments (Figure 1.2), 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), I considered further sub-division unnecessary. Spatial groups (g) were next defined as sets of one or more of these coastline segments: I 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:

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

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), I could allow for three or four grouping levels. I 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, I 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). I 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 my 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. My 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. The baseline values for age-specific weaning success were derived from data reported by Riedman and Estes (1994). To create a smoothed w' vector, I fit a single-parameter logit function to their point estimates:

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

where γ is the fitted parameter ($\gamma = 0.01548$, 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:

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

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). I 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: I will hereafter refer to a particular model form as M_i ($i = 1, 2 \dots I$, where I is the total possible number of unique model forms). Each unique model, M_i , will have an associated vector of model parameters, θ_i ($\theta_i = [\theta_1, \theta_2 \dots \theta_n]$);

the length of vector θ 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

I 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). I 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 in this case 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), I calculated the expected number surviving to time $t+1$ as:

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

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

$$D_{x,y,t,g}^{\text{exp}} = N_{x,y,t,g} - N_{x+1,y,t+1,g} \quad 10$$

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, I combined the vital rates b and w in order to express reproduction as $R_{x,t,g \rightarrow y}$, 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, $R_{x,t,g \rightarrow y}$ 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 I wished also to keep track of the expected number of dependant pups at time $t+1$ (for comparison with the annual pup counts), I instead divided $R_{x,t,g \rightarrow y}$ into two components: $R_{x,t,g \rightarrow y}^1$ the probability of producing a pup that successfully weans and survives as an independent juvenile at $t+1$, and $R_{x,t,g \rightarrow y}^2$, 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: I assume that birth probabilities are divided approximately equally between these two groups.

For the first component of reproduction, $R^1_{x,t,g \rightarrow y}$, I consider a typical female to be one that produces a pup exactly 3 months after the census. Such a female must survive for $\frac{3}{4}$ of the year if her pup is to be weaned successfully, and the weaned pup must then survive for the remaining $\frac{1}{4}$ of the year as an independent juvenile. I assumed that the post-weaning survival rate was equal to the survival rate for the subsequent juvenile year class, and calculated $R^1_{x,t,g \rightarrow y}$ as:

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

Calculation of the second component of reproduction, $R^2_{x,t,g \rightarrow y}$, 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:

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

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, I used equation 12 to calculate $R^2_{x,t,g \rightarrow y}$ as:

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

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

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

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:

$$P^{\text{exp}}_{t+1,g} = \sum_{y=1}^2 \sum_{x=1}^{20} N_{x,0,t+1,g} \cdot R^2_{x,t,g \rightarrow y} \quad 15$$

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 $t=1$. I 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 1.1), presumably allowing demographic rates to stabilize. For all subsequent years, I 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:

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

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

$$\ell(C_{y,t,g}^{\text{obs}} | M_{i,j}) = \frac{N!}{C_1! C_2! \dots C_x!} d_1^{C_1} \cdot d_2^{C_2} \cdot \dots d_x^{C_x} \quad 17$$

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 $\ell(C^{\text{obs}} | M_{i,j})$ estimates.

To calculate the relative likelihood of observed population counts, I 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). I 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, $M_{i,j}$, I calculated the likelihood of observed counts of independents, N^{obs} , as:

$$\ell(N^{obs} | M_{i,j}) = \frac{1}{\sqrt{2 \cdot \pi \cdot \sigma_N^2}} \cdot e^{\left(-1 \cdot \frac{(N^{obs} - N^{exp})^2}{2 \cdot \sigma_N^2}\right)} \quad 18$$

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

$$\ell(P^{obs} | M_{i,j}) = \frac{1}{\sqrt{2 \cdot \pi \cdot \sigma_P^2}} \cdot e^{\left(-1 \cdot \frac{(P^{obs} - P^{exp})^2}{2 \cdot \sigma_P^2}\right)} \quad 19$$

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, I converted all likelihood values to negative log-likelihoods ($\mathbf{L} = -\log(\ell)$) and instead calculated the sum of the associated \mathbf{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 L . To perform model fits I used a box-bounded, global optimization routine based on the DIRECT modification of the Lipschitzian minimization algorithm (Jones et al. 1993). Note that I 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, I 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 L , but this measurement alone provides a poor indication of the robustness or utility of a particular model (Hilborn and Mangel 1997). I used information theory criterion to compare and select models, and to formally account for model uncertainty in my final, overall estimates of demographic parameters (Burnham and Anderson 1998).

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

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

where $L_{i,min}$ 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, I 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). I limited consideration to the sub-set of Z models having Δ_i values below a cut-off value, Δ_{crit} , which I initially set to 10 (Burnham and Anderson 1998). Finally, for each of the Z models considered, I calculated Akaike weights, α_i as:

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

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 my model formulation presented a severe computational challenge. Rather than finding maximum likelihood solutions for every possible combination of functional form and spatial grouping scheme, I 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), I conducted maximum likelihood analysis for all combinations of spatial grouping schemes. I 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 1.3). I 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 . I then applied Δ_{crit} to identify the Z models to be used for subsequent analysis.

I next calculated model-averaged estimates of all demographic rates, as well as the associated unconditional variance estimates. To simplify presentation, I 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 ($L_{i,min}$). 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):

$$\Pr(S_{i,j}) \cong \Pr(\chi_{df=1}^2 \geq 2 \cdot (L_{i,j} - L_{i,min})) \quad 22$$

I 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. I then calculated a model-specific variance estimate for S_i as:

$$\text{var } S_i = \frac{1}{\sum_{j=1}^J \text{Pr}(S_{i,j})} \cdot \sum_{j=1}^J \text{Pr}(S_{i,j}) \cdot (S_{i,j} - \hat{S}_i)^2 \quad 23$$

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

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

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

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

The model averaged estimates for weaning success rates, as well as their associated unconditional variance estimates, were calculated in an analogous fashion. I 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, I 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 1.2).

Demographic rates and their unconditional variance estimates were calculated for 20 year classes; however, for presentation purposes I 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{S}_a and \hat{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). I 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, $x = 1, 2 \dots n$) of:

$$\text{var } \bar{S}_a = \begin{bmatrix} \partial \hat{S}_a / \partial \hat{S}_1 & \partial \hat{S}_a / \partial \hat{S}_2 & \cdots & \partial \hat{S}_a / \partial \hat{S}_n \end{bmatrix} \bullet \begin{bmatrix} \text{var } \bar{S}_1 & \text{cov } \bar{S}_1 \bar{S}_2 & \cdots & \text{cov } \bar{S}_1 \bar{S}_n \\ \text{cov } \bar{S}_1 \bar{S}_2 & \text{var } \bar{S}_2 & \cdots & \text{cov } \bar{S}_2 \bar{S}_n \\ \vdots & \vdots & \ddots & \vdots \\ \text{cov } \bar{S}_1 \bar{S}_n & \text{cov } \bar{S}_2 \bar{S}_n & \cdots & \text{var } \bar{S}_n \end{bmatrix} \bullet \begin{bmatrix} \partial \hat{S}_a / \partial \hat{S}_1 \\ \partial \hat{S}_a / \partial \hat{S}_2 \\ \vdots \\ \partial \hat{S}_a / \partial \hat{S}_n \end{bmatrix} \quad 26$$

where $\partial \hat{S}_a / \partial \hat{S}_x$ was set to $1/n$ for all year classes (i.e. I 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.

I 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:

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

where:

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

and where $\text{var } \bar{p}$ 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).

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

Between October 2000 and September 2003, a total of 115 adult sea otters were captured and tagged 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, I intentionally biased sampling to capture mostly adults: consequently, sample sizes are too low at this time to allow estimation of survival 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).

I partitioned my 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 females were not captured 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 me 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, I restrict my 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).

I analyzed survival data using a Kaplan-Meier “known-fates” model that allows for staggered entry of study animals (Pollock et al. 1989), and I conducted all computations using Program MARK (White and Burnham 1999). I 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). I 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, I 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. I used model averaging to incorporate model uncertainty into the final estimates (see methods for Part 1, Burnham and Anderson 1998).

I 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. I calculated mean birth rate using the “direct method” (sensu Eberhardt and Schneider 1994):

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

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, I 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 1.4). Reducing $\Delta_{i,crit}$ (the cut-off value for model consideration) down to 5 had no measurable effect on model-averaged vital rate estimates; I therefore re-set $\Delta_{i,crit}$ to 5, restricting subsequent analyses to the 34 best-supported models (Appendix A).

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 1.5). 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) I report all further results for females only.

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 ($CI_{95} = 0.48\text{--}74$). 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 1.6). 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 ($CI_{95} = 0.83\text{--}90$) in 1992 but decreased to 0.84 ($CI_{95} = 0.77\text{--}89$) 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 1.7). 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.

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 1.7). 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 1.8), decreased survival of prime-age adults likely contributed most to the observed change in population growth over the 1990's.

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 1.9A). Interestingly, there was greater disparity between expected and observed counts when plotted separately for the four major geographic regions (Figure 1.9B). 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.

Results, 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 1.1), consistent with the spatial patterns reported in Part 1 (Figure 1.6). In the Monterey and San Simeon study areas, survival during the summer months was lower than fall and winter (Figure 1.10); 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.

The recent survival rates reported here for adult females are considerably lower than the estimates reported from the 1980's (Table 1.1), 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 1.1). 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 1.11).

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 1.11). 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. I 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, my 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 1.10) 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 1.7). 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 1.8): 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.

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).

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 1.9A); however, the lack of close fit between expected and observed counts within each geographic region (Figure 1.9B) 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 1.9B), 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 the 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 1.11) 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 prediction that would seem to be countered by an apparent stabilization of population numbers in recent years (Figure 1.1). 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 1.6, Table 1.1) 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 my methodology have broader implications for population analyses of other species. First, I 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, my 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 I am using an information theoretic approach in an exploratory way here; I am 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, the methodological approach described in Part 1 is in grave danger of violation because I consider such a large suite of possible model forms. I 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 I 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, my 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). I 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.

Tables

Table 1.1 Maximum Likelihood model-averaged estimates of annual survival rates for adult sea otters, derived from telemetry-based, mark-recapture data.

<u>Sex/Study Group</u>	<u>Mean</u>	<u>SE</u>	<u>L95</u>	<u>U95</u>
<u>Females</u>				
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
<u>Males</u>				
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

¹ estimates reported by Siniff and Ralls (1991).

Figures

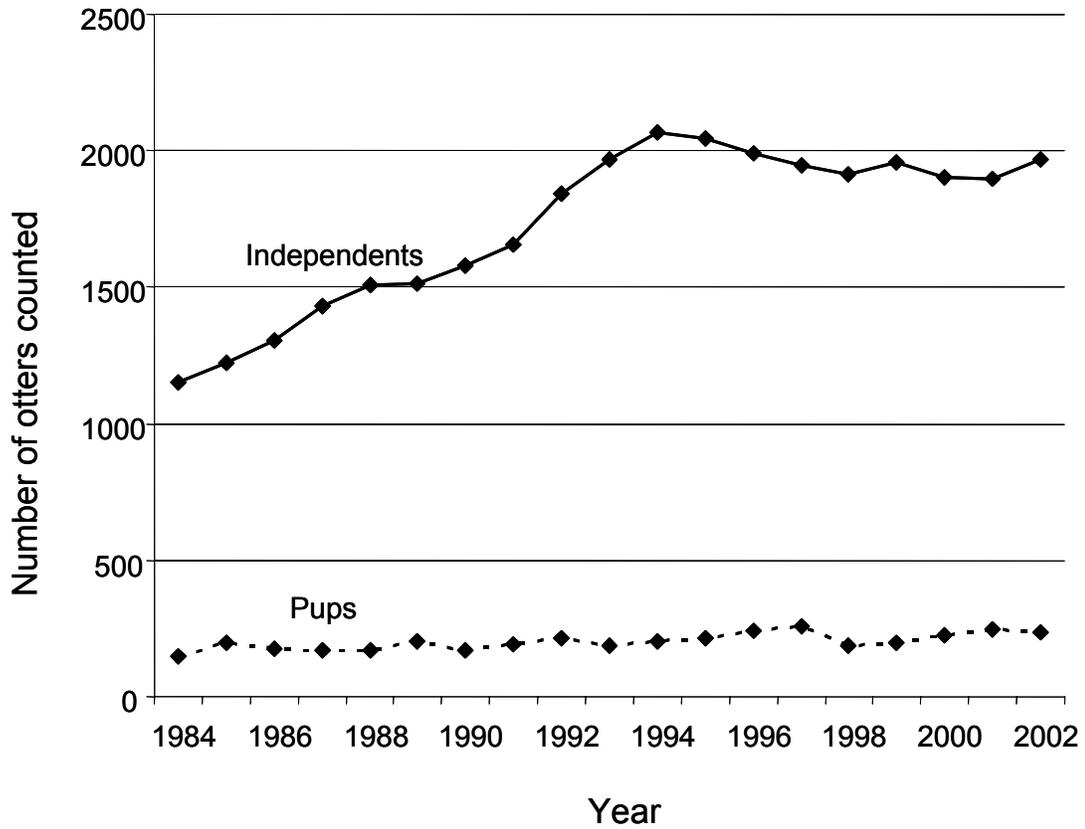


Figure 1.1. Annual range-wide counts of southern sea otters, *Enhydra lutris nereis*, conducted between 1984 and 2002. Values represent the three-year running average of the spring counts of independents (solid line) and the annual average of the spring and fall counts of dependent pups (dashed line).

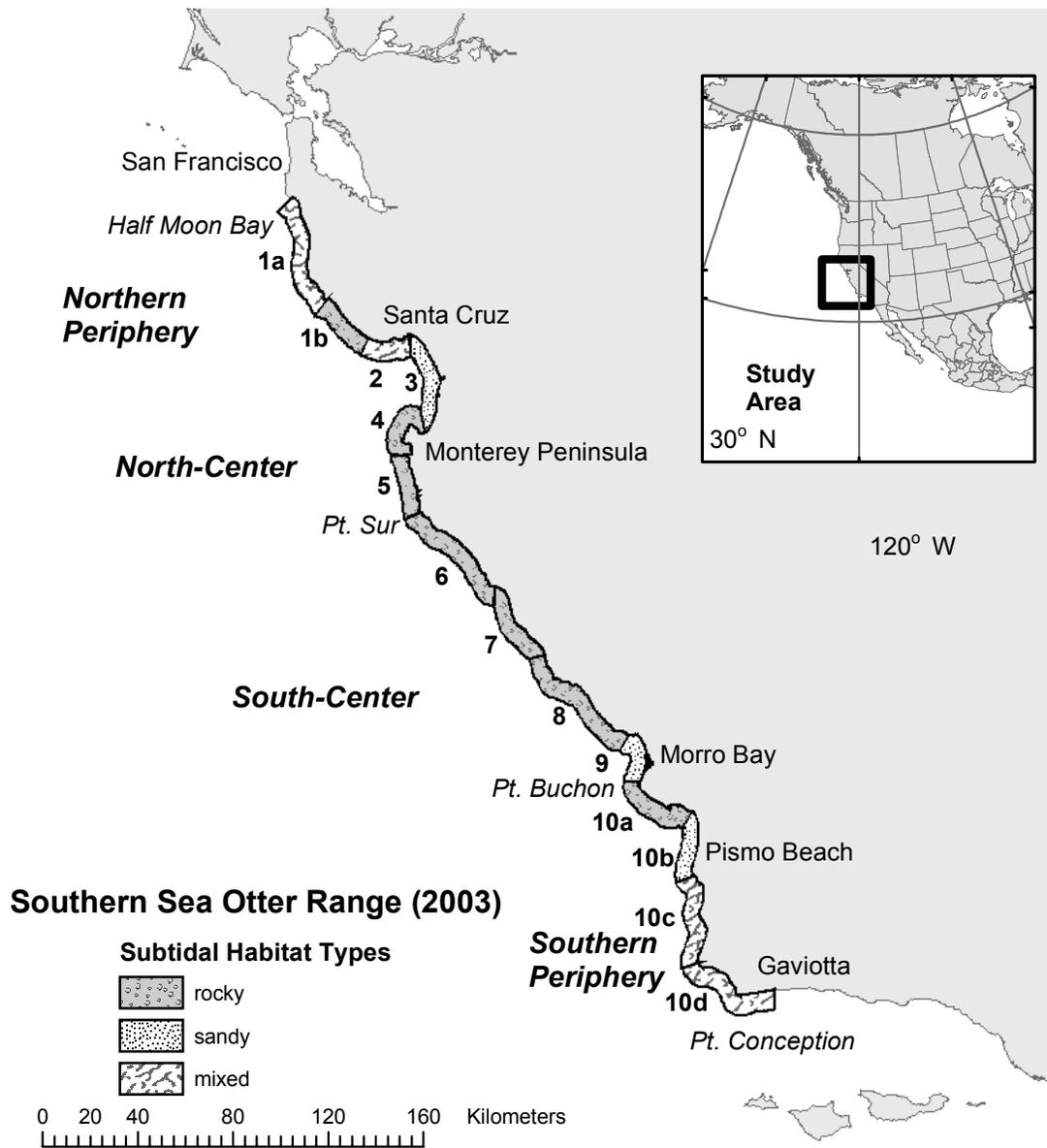


Figure 1.2. Range of the southern sea otter along the mainland coast of California (range limits based on 2003 survey data) divided into 14 sections of similar sub-tidal habitat (Laidre et al. 2001). These sections were used as fundamental geographical units for my analysis of spatial variation in demography, 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).

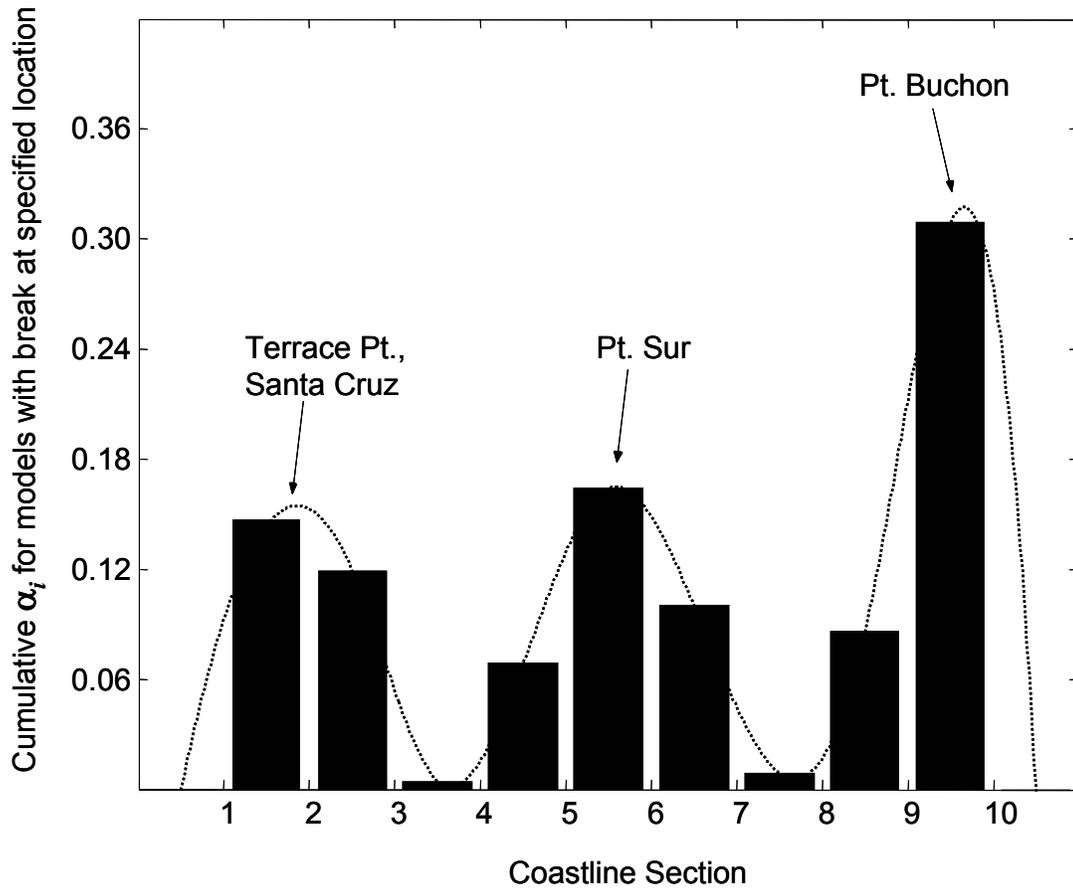


Figure 1.3. The relative degree of model support for all potential arrangements of 10 coastline sections into areas of similar demography. Summed AIC weights (α_i values) are shown at each potential break-point: the three peaks of the resulting distribution correspond to the best-supported break locations.

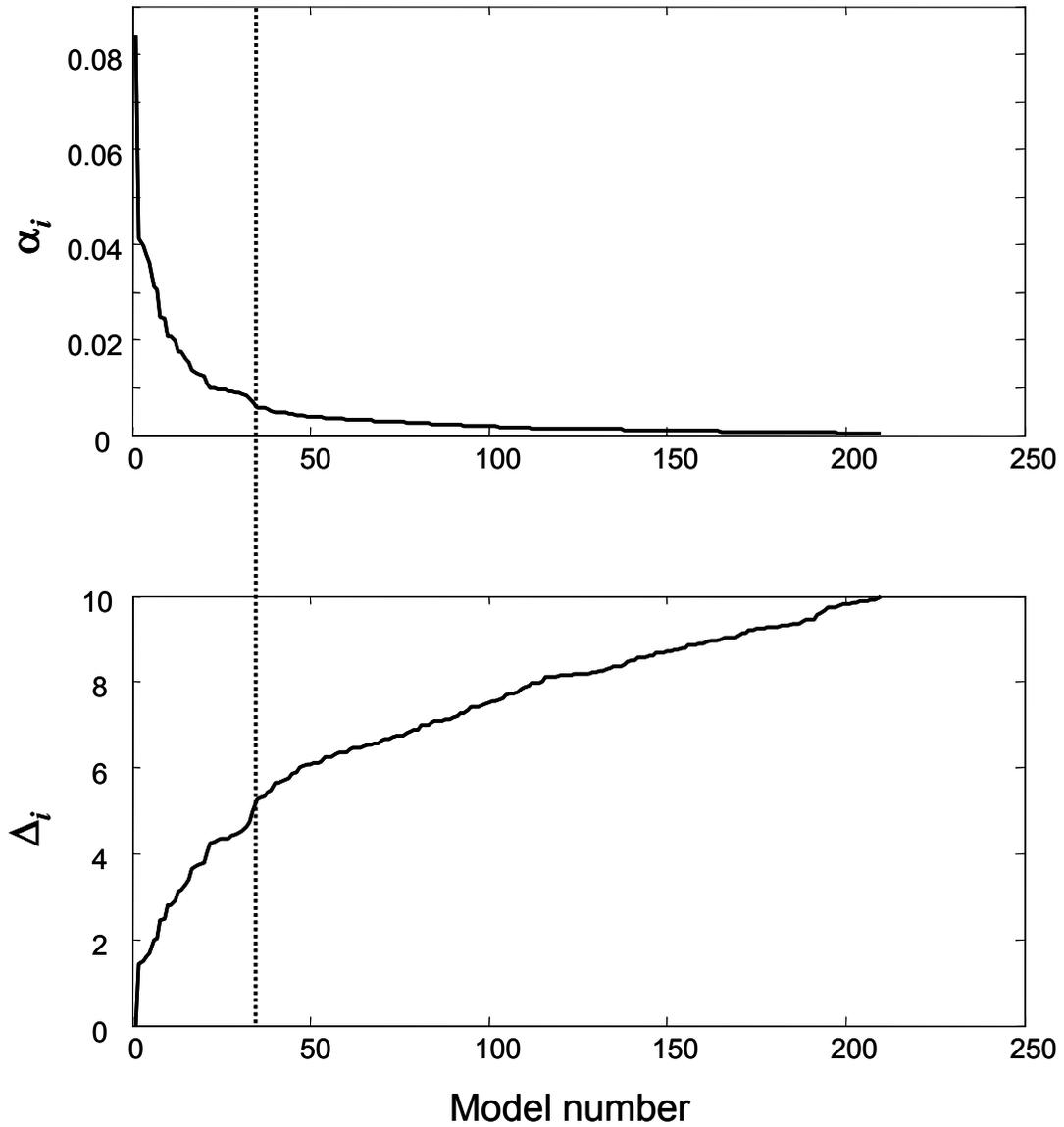


Figure 1.4. Profiles of AIC weights (α_i values, top graph) and Δ_i values (bottom graph) for the 210 models with $\Delta_i \leq 10$. The α_i values approach an asymptote after model 35 (indicated by dotted line), which also corresponds to the final cut-off value ($\Delta_i = 5$) used to select models for inclusion in model averaging.

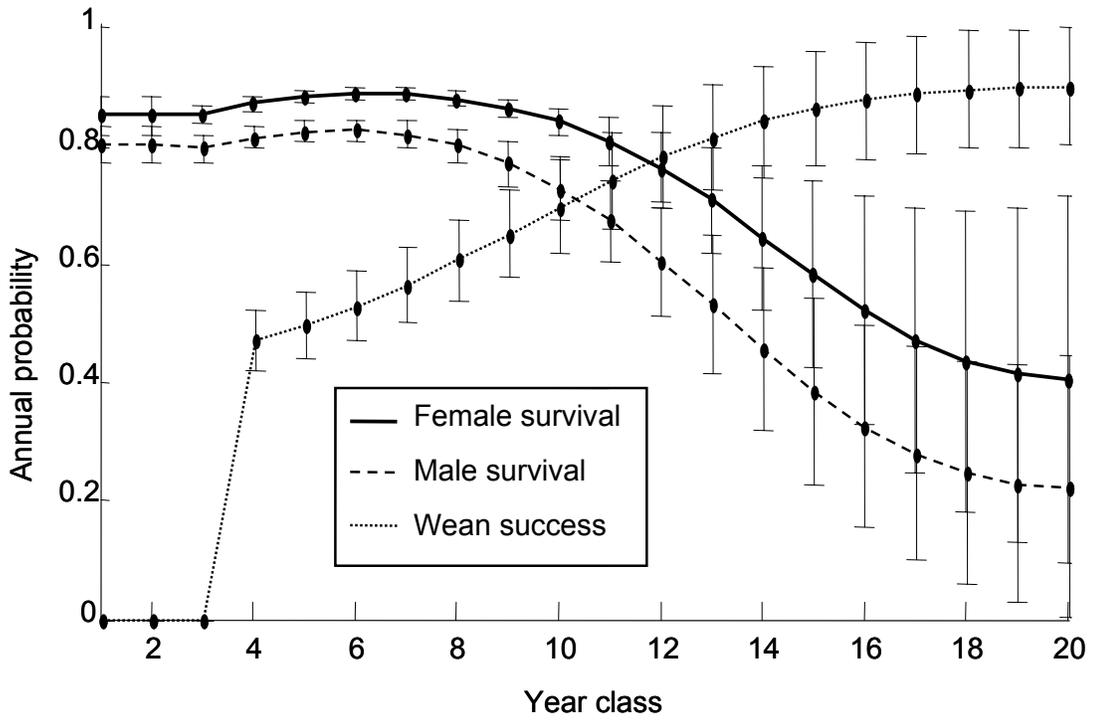


Figure 1.5. The Age-specific schedule of annual survival rates for females (solid line) and males (dashed line), as well as weaning success rates (dotted line). Model-averaged estimates and their standard errors are shown for 1992 in the north-center of the range.

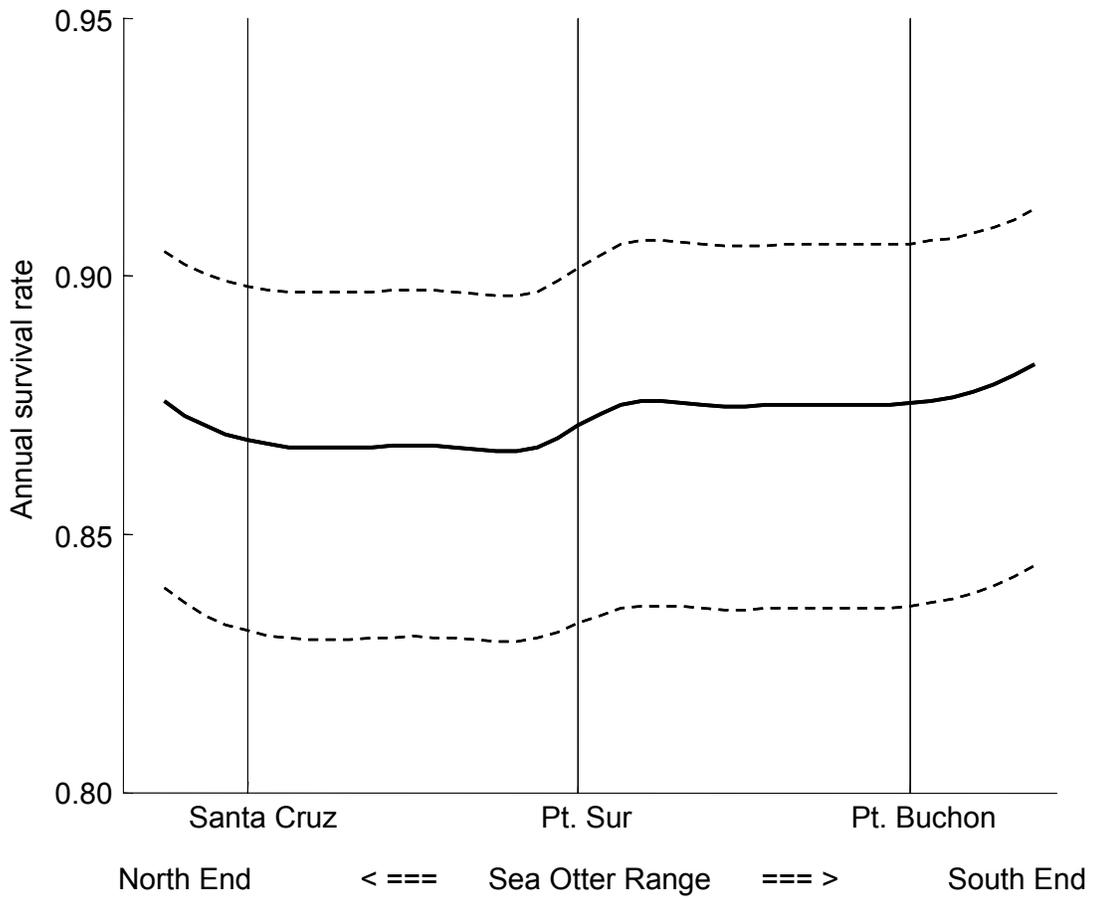


Figure 1.6. Spatial variation in the annual survival rate of adult females. Center curve shows the model-averaged rate for 1992, while dashed lines indicate the unconditional 95% confidence bounds.

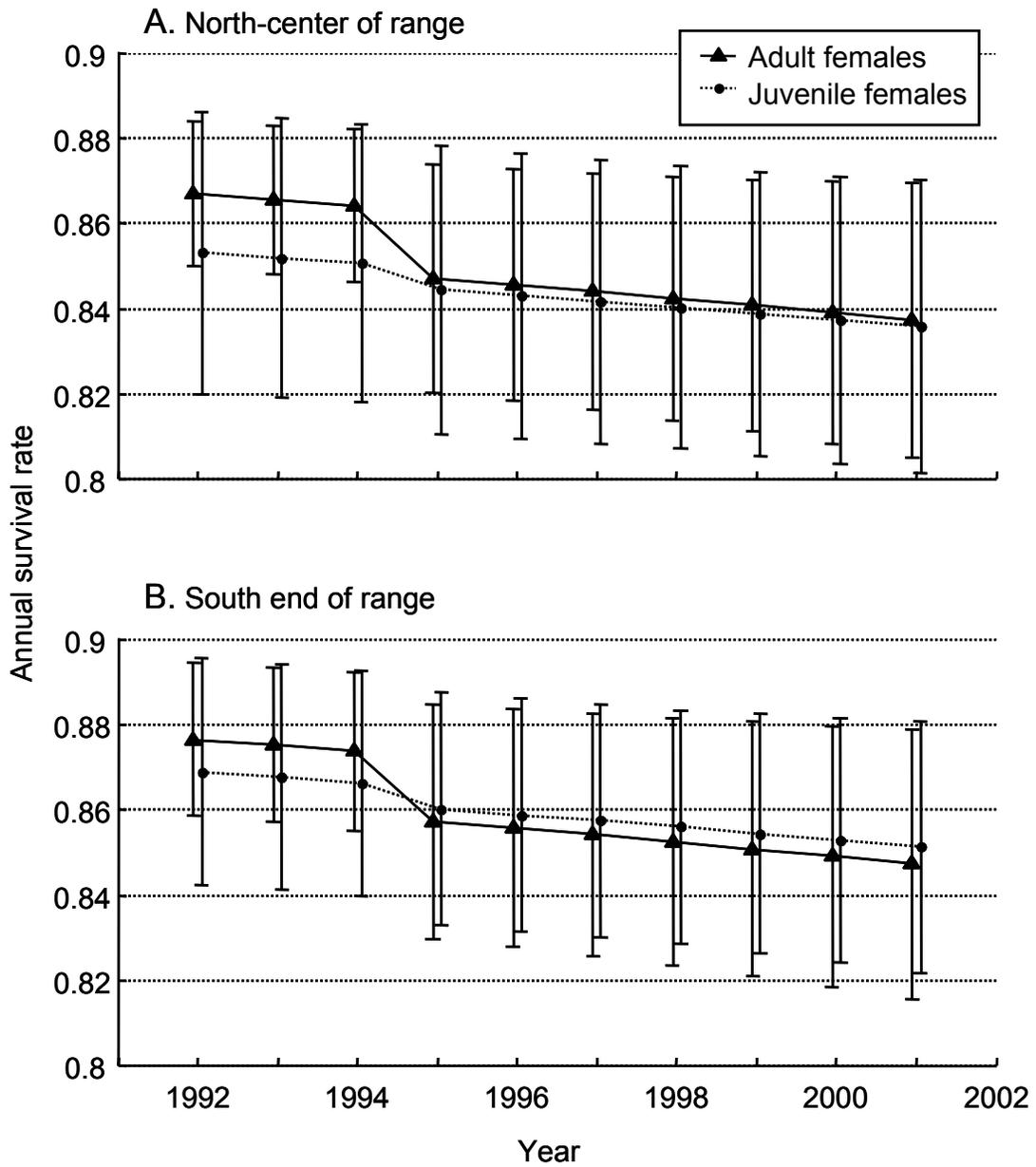


Figure 1.7. Temporal variation in the annual survival rate of adult females (solid lines) and juvenile females (dashed lines). A) Estimated survival rates for 1992-2001 in the north-center of the range; B) estimated survival rates for 1992-2001 in the southern periphery of the range.

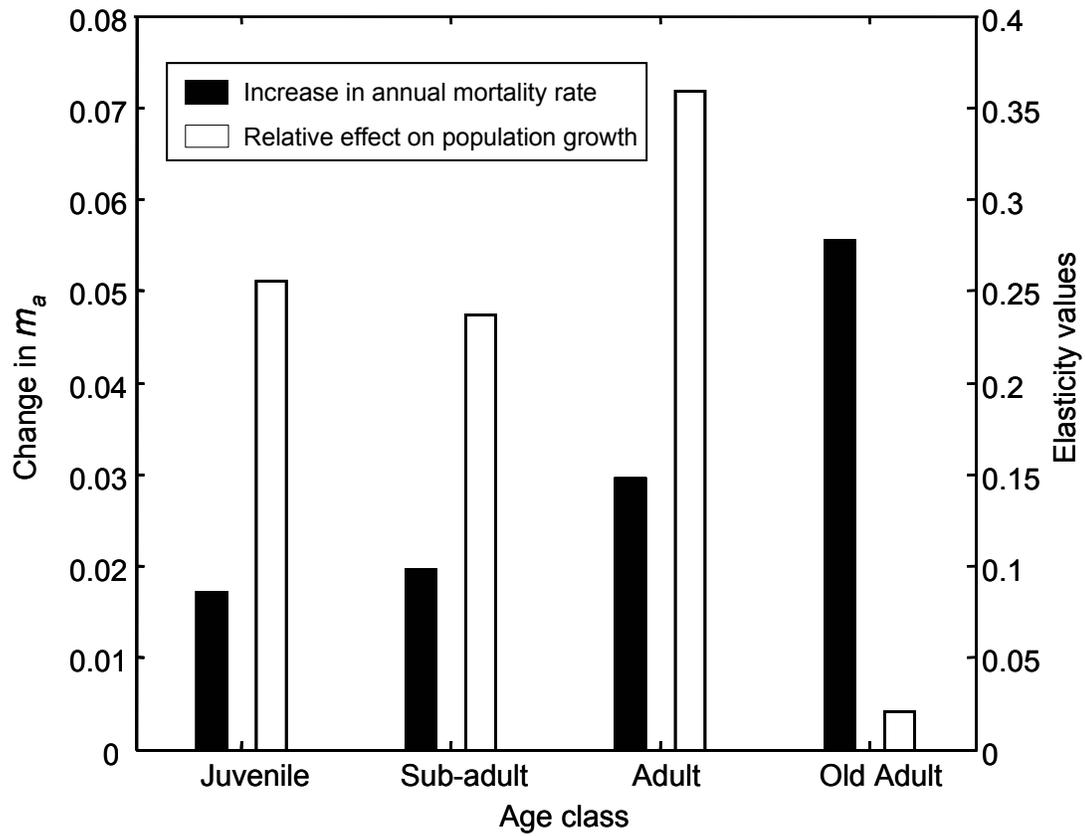


Figure 1.8. Increase in annual mortality rates ($m_a = 1 - S_a$) between 1992 and 2001 (black bars) and corresponding survival elasticity values (white bars) for 4 female age classes: juveniles, sub-adults, adults and old adults. Elasticity values were derived algebraically from the 1992 matrix and summed for each age class.

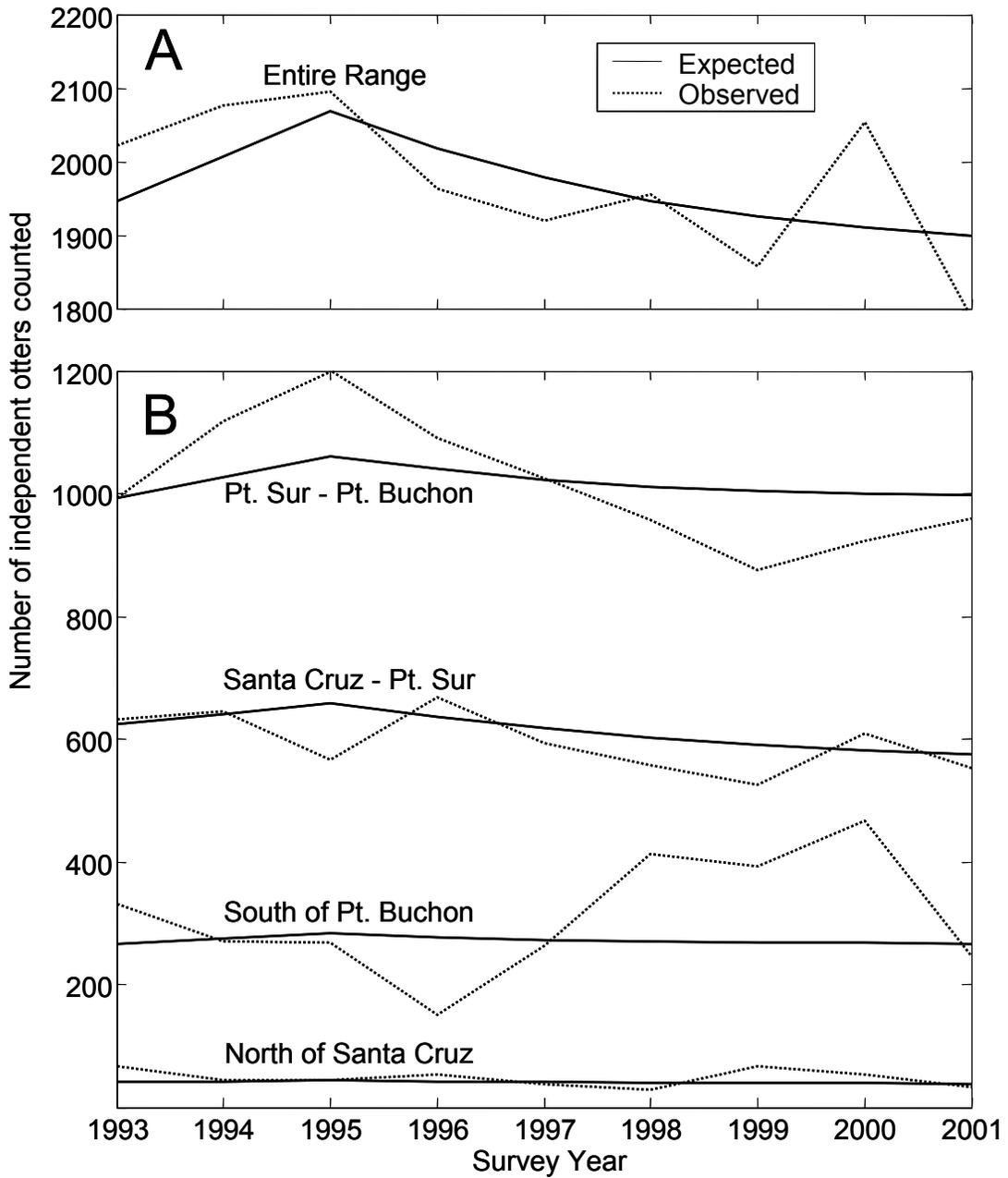


Figure 1.9. Expected trends in population abundance between 1993 and 2001, as predicted by matrix projections using the maximum likelihood estimated vital rates. Observed population counts are plotted for comparison. A) Expected vs. observed counts for the entire population; B) expected vs. observed counts for 4 major geographic sub-divisions of the range.

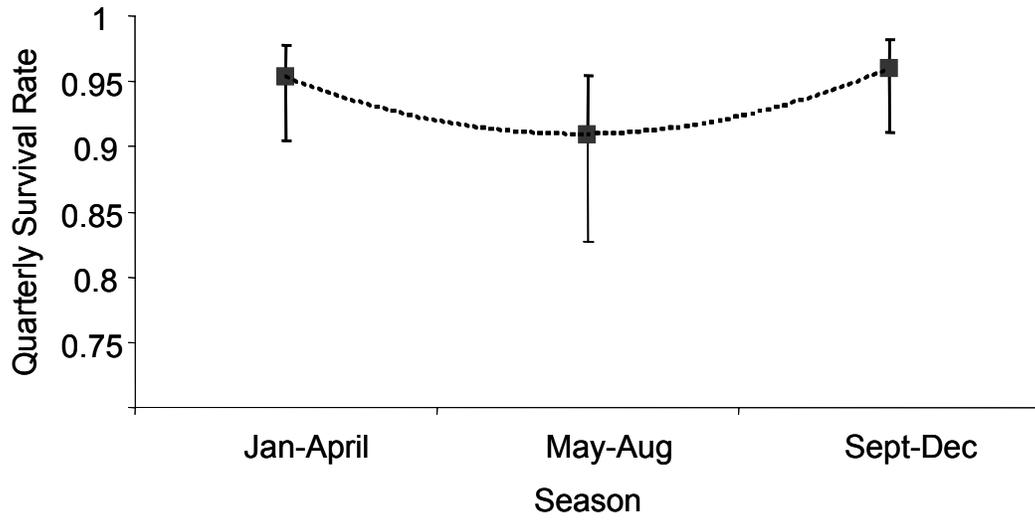


Figure 1.10. Seasonal variation in survival probabilities for adult females in the center of the range, as estimated from mark-recapture data. Model-averaged estimates of quarterly survival are shown, spanned by their 95% confidence intervals.

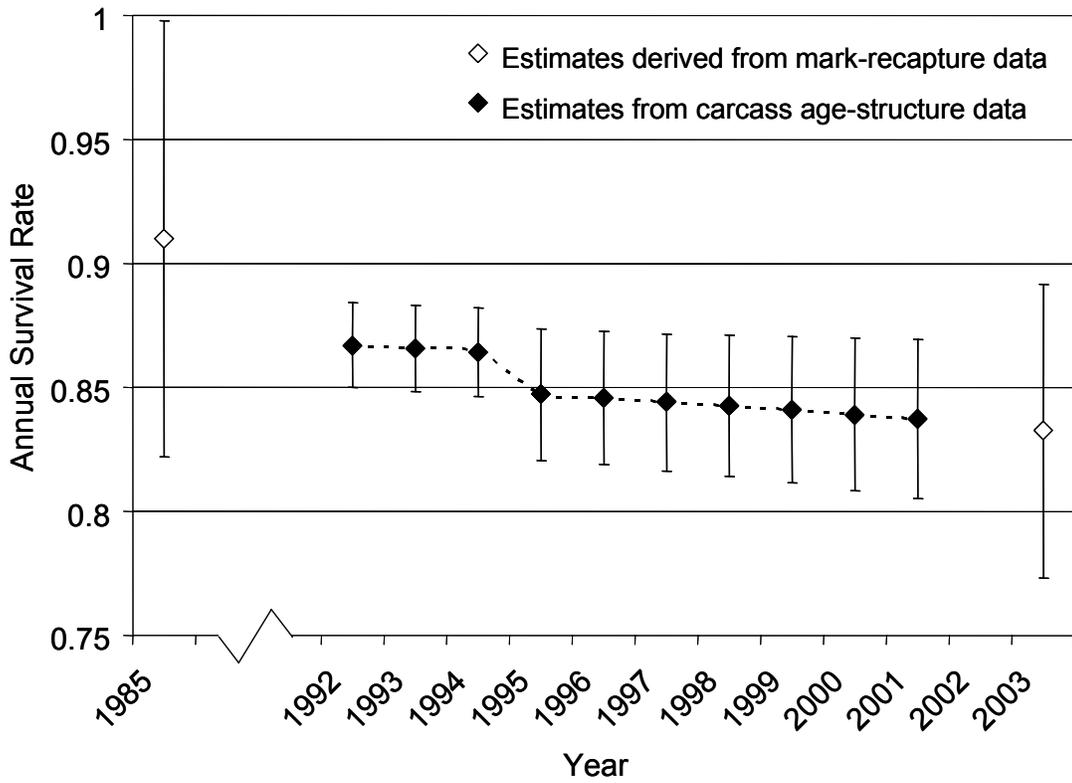


Figure 1.11. Synthesis of survival estimates derived from two independent analyses and data sets, summarizing the inferred temporal changes in adult female survival in the center of the range. The 1985 estimate is that reported by Siniff and Ralls (1991).

References

- Akaike, H. 1973. Parameter estimation for models of chaotic time series. *Journal of Mathematical Biology* **30**:839-852.
- Ames, J. A., R. A. Hardy, F. E. Wendell, and J. J. Geibel. 1983. Sea otter mortality in California. Marine Resources Branch, California Department of Fish and Game.
- Bodkin, J. L., J. A. Ames, R. J. Jameson, A. M. Johnson, and G. M. Matson. 1997. Estimating age of sea otters with cementum layers in the first premolar. *Journal of Wildlife Management* **61**:967-973.
- Bodkin, J. L., A. M. Burdin, and D. A. Ryazanov. 2000. Age- and sex-specific mortality and population structure in sea otters. *Marine Mammal Science* **16**:201-219.
- Burgman, M. A., S. Ferson, and H. R. Akcakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, London, UK.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York, NY.
- Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, 2nd ed edition. Sinauer Associates, Sunderland, MA.
- Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, NY.
- Coulson, T., S. Albon, J. Pilkington, and T. Clutton-Brock. 1999. Small-scale spatial dynamics in a fluctuating ungulate population. *Journal of Animal Ecology* **68**:658-671.
- Crooks, K. R., M. A. Sanjayan, and D. F. Doak. 1998. New insights on cheetah conservation through demographic modeling. *Conservation Biology* **12**:889-895.
- Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. *Ecology* **68**:1412-1423.
- Doak, D. F. 1995. Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. *Conservation Biology* **9**:1370-1379.
- Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. *Ecology* **75**:615-626.
- Doak, D. F., and W. Morris. 1999. Detecting population-level consequences of ongoing environmental change without long-term monitoring. *Ecology* **80**:1537-1551.

- Doak, D. F., and W. F. Morris. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, MA.
- Eberhardt, L. L. 1985. Assessing the dynamics of wild populations. *Journal of Wildlife Management* **49**:997-1012.
- Eberhardt, L. L. 1988. Using age structure data from changing populations. *Journal of Applied Ecology* **25**:373-378.
- Eberhardt, L. L. 1995. Using the Lotka-Leslie model for sea otters. *Journal of Wildlife Management* **59**:222-227.
- Eberhardt, L. L., B. M. Blanchard, and R. R. Knight. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. *Canadian Journal of Zoology* **72**:360-363.
- Eberhardt, L. L., and K. B. Schneider. 1994. Estimating sea otter reproductive rates. *Marine Mammal Science* **10**:31-37.
- Eberhardt, L. L., and D. B. Siniff. 1988. Population model for Alaska Peninsula sea otters. MMS 88-0091, U.S. Department of Interior, Minerals Management Service, OCS Study, Anchorage.
- Estes, J. A., B. B. Hatfield, K. Ralls, and J. Ames. 2003. Causes of mortality in California sea otters during periods of population growth and decline. *Marine Mammal Science* **19**:198-216.
- Estes, J. A., and R. J. Jameson. 1988. A double-survey estimate for sighting probability of sea otters in California. *Journal of Wildlife Management* **52**:70-76.
- Forsman, E. D. 1993. Demographic studies of northern spotted owls. *Journal of Raptor Research* **27**:54-55.
- Gerber, L. R., T. Tinker, D. Doak, and J. Estes. *in press*. Mortality sensitivity in life-stage simulation analysis: A case study of southern sea otters. *Ecological Applications*.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, NJ.
- Holmström, K. 1999. The Tomlab optimization environment in Matlab. *Advanced Modeling and Optimization* **1**:47-69.
- Jameson, R. J. 1989. Movements, home range, and territories of male sea otters off central California. *Marine Mammal Science* **5**:159-172.
- Jameson, R. J., and A. M. Johnson. 1993. Reproductive characteristics of female sea otters. *Marine Mammal Science* **9**:156-167.

- Jones, D. R., C. D. Perttunen, and B. E. Stuckman. 1993. Lipschitzian optimization without the Lipschitz constant. *Journal of Optimization Theory and Applications* **79**:157–181.
- Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. *North American Fauna* **68**:1-352.
- Kreuder, C., M. A. Miller, D. A. Jessup, L. J. Lowenstine, M. D. Harris, J. A. Ames, T. E. Carpenter, P. A. Conrad, and J. A. K. Mazet. 2003. Patterns of mortality in southern sea otters (*Enhydra lutris nereis*) from 1998-2001. *Journal of Wildlife Diseases* **39**:495-509.
- Laidre, K. L., R. J. Jameson, and D. P. DeMaster. 2001. An estimation of carrying capacity for sea otters along the California coast. *Marine Mammal Science* **17**:294-309.
- Lande, R. 1991. Population dynamics and extinction in heterogeneous environments: the northern spotted owl. Pages 566-580 in C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, editors. *Oxford Ornithology Series, Vol. 1. Bird Population Studies: Relevance to Conservation and Management; Symposium, La Camargue, France, December 12-16, 1988*. Oxford University Press, Oxford, England, UK.
- Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* **33**:183-212.
- Matson, G. M. 1981. Workbook for cementum analysis. Matson's Laboratory, Milltown, MT.
- McCleneghan, K., and J. A. Ames. 1976. A unique method of prey capture by the sea otter, *Enhydra lutris* Linnaeus. *Journal of Mammalogy* **57**:410-412.
- Miller, M. A., I. A. Gardner, C. Kreuder, D. M. Paradies, K. R. Worcester, D. A. Jessup, E. Dodd, M. D. Harris, J. A. Ames, A. E. Packham, and P. A. Conrad. 2002. Coastal freshwater runoff is a risk factor for *Toxoplasma gondii* infection of southern sea otters (*Enhydra lutris nereis*). *International Journal for Parasitology* **32**:997-1006.
- Milner-Gulland, E. J., T. N. Coulson, and T. H. Clutton-Brock. 2000. On harvesting a structured ungulate population. *Oikos* **88**:592-602.
- Monson, D. H., D. F. Doak, B. E. Ballachey, A. Johnson, and J. L. Bodkin. 2000a. Long-term impacts of the Exxon Valdez oil spill on sea otters, assessed through age-dependent mortality patterns. *Proceedings of the National Academy of Sciences of the United States of America* **97**:6562-6567.
- Monson, D. H., J. A. Estes, J. L. Bodkin, and D. B. Siniff. 2000b. Life history plasticity and population regulation in sea otters. *Oikos* **90**:457-468.

- Monson, D. H., C. McCormick, and B. E. Ballachey. 2001. Chemical anesthesia of northern sea otters (*Enhydra lutris*): results of past field studies. *Journal of Zoo & Wildlife Medicine* **32**:181-189.
- Pascual, M. A., and M. D. Adkison. 1994. The decline of the Steller sea lion in the northeast Pacific: demography, harvest or environment? *Ecological Applications* **4**:393-403.
- Pascual, M. A., P. Kareiva, and R. Hilborn. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. *Conservation Biology* **11**:966-976.
- Pattison, C. A., M. D. Harris, and F. E. Wendell. 1997. Sea Otter, *Enhydra lutris*, mortalities in California, 1968 through 1993. Administrative Report 97-5, Marine Resources Branch, California Fish and Game., Morro Bay, CA.
- Pease, C. M., and D. J. Mattson. 1999. Demography of the Yellowstone grizzly bears. *Ecology* **80**:957-975.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences of the United States of America* **95**:213-218.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* **107**:1-98.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* **53**:7-15.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**:652-661.
- Ralls, K., T. C. Eagle, and D. B. Siniff. 1996. Movement and spatial use patterns of California sea otters. *Canadian Journal of Zoology* **74**:1841-1849.
- Riedman, M. L., J. A. Estes, M. M. Staedler, A. A. Giles, and D. R. Carlson. 1994. Breeding patterns and reproductive success of California sea otters. *Journal of Wildlife Management* **58**:391-399.
- Schaefer, J. A., A. M. Veitch, F. H. Harrington, W. K. Brown, J. B. Theberge, and S. N. Luttich. 2001. Fuzzy structure and spatial dynamics of a declining woodland caribou population. *Oecologia* **126**:507-514.
- Schoen, R. 1988. Modeling multigroup populations. Plenum Press, New York, NY.
- Siler, W. 1979. A competing-risk model for animal mortality. *Ecology* **60**:750-757.

- Sinha, A. A., C. H. Conaway, and K. W. Kenyon. 1966. Reproduction in the female sea otter. *Journal of Wildlife Management* **30**:121-130.
- Siniff, D. B., and K. Ralls. 1988. Population status of California sea otters: MMS 14-12-001-30033. U.S. Department of Interior, Minerals Management Service, California.
- Siniff, D. B., and K. Ralls. 1991. Reproduction, survival and tag loss in California sea otters. *Marine Mammal Science* **7**:211-229.
- Thomas, N. J., and R. A. Cole. 1996. The risk of disease and threats to the wild population. *Endangered Species Update* **13**:23-27.
- Udevitz, M. S., and B. E. Ballachey. 1998. Estimating survival rates with age-structure data. *Journal of Wildlife Management* **62**:779-792.
- USFWS. 2003. Final revised recovery plan for the southern sea otter (*Enhydra lutris nereis*). U.S. Fish and Wildlife Service. Portland, OR.
- Watt, J., D. B. Siniff, and J. A. Estes. 2000. Inter-decadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska. *Oecologia* **124**:289-298.
- Wendell, F. E., J. A. Ames, and R. A. Hardy. 1984. Pup dependency period and length of reproductive cycle: estimates from observations of tagged sea otters, *Enhydra lutris*, in California. *California Fish and Game* **70**:89-100.
- White, G. C. 1983. Numerical estimation of survival rates from band recovery and biotelemetry data. *Journal of Wildlife Management* **47**:716-728.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**:S120-S139.
- Williams, T., and D. B. Siniff. 1983. Surgical implantation of radio telemetry devices in the sea otter. *Journal of the American Veterinary Medical Association* **11**:1290-1291.

Chapter 2. Alternative foraging strategies in southern sea otters

Introduction

Intraspecific variation in diet and foraging behavioral strategies is a characteristic of many animal populations (Partridge and Green 1985, Bolnick et al. 2003). Conspecifics may utilize different foraging strategies for a variety of reasons: morphological or physiological differences (Smith 1987, Barbosa et al. 2000), geographic variation or habitat differences (Kruuk and Moorhouse 1990, Tanaka 1991), sex-, age- or stage-dependent strategies (Clarke et al. 1998, Reinhardt and Healey 1999) and frequency-dependant variation (Beauchamp et al. 1997) have all been documented. 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). Alternative foraging strategies are often associated with genetically-maintained polymorphisms (Skúlason and Smith 1995), but distinct behavioral strategies may also exist without any clear genetic basis (Clark and Ehlinger 1973). For example, cultural transmission of individual foraging strategies can result in distinct behavioral morphs that persist over generations and have dynamics that are quantitatively and qualitatively similar to those reported for genetically transmitted polymorphisms (e.g. Sutherland et al. 1996, Estes et al. 2003b).

Individual differences in diet and feeding behavior that are not associated with genetically-maintained polymorphisms are interesting because foraging behavior is thought to be under strong selection due to its direct impact on fitness (Emlen 1966, MacArthur and

Pianka 1966, Pyke et al. 1977, Mangel and Clark 1988). This is particularly true for food-limited predators: that is, species for which the relative abundance of prey resources is the dominant factor limiting population growth (in contrast to species that are primarily limited by space, suitable nesting sites or predators). Questions raised by the existence of multiple foraging strategies focus primarily on the implications for individual fitness: how do different strategies compare with regards to their rate of energy return, are they associated with environmental variation (e.g. spatial or temporal differences in prey abundance), and what mechanisms prevent convergence on a single “optimal” strategy? Here I use the term “foraging strategy” to refer to a distinct pattern of diet composition and foraging behavior that can be easily distinguished from other such patterns. Note that this is qualitatively different from purely random variation between individuals, which can be explained by environmental stochasticity in combination with additive variation in the phenotype of individual foragers and random sampling effects. Random variation in diet composition and feeding behavior is to be expected even if all individuals are selected to use a single strategy: in contrast, alternative strategies represent distinct and fundamentally different solutions to the problem of energy acquisition (Clark and Ehlinger 1973).

The co-existence of multiple diet types or foraging strategies is especially puzzling if these strategies do not provide an equal rate of energy gain. Such differentials may be adaptive if there are other costs or benefits, such as lower predation risk, that increase the net realized fitness of apparently sub-optimal strategies (Abrams 1993, Clark and Mangel 2000). Another mechanism that may serve to maintain multiple strategies in a population is the existence of local fitness optima: that is, each mode of behavior or diet type corresponds to a peak in a “fitness surface”, while intermediate points have lower values and thus lie in

“valleys” (Smith 1987, Benkman 1993). A fitness surface is simply a graphic representation of the shape of selective pressures on one or more phenotypic traits (Schluter 1988, Sinervo 2000). The forces generating and maintaining behavioral polymorphisms are likely to be the same as for genetic polymorphisms: correlational selection on suites of interacting traits generates multiple fitness optima (Sinervo and Svensson 2002), and the distinct behavioral strategies corresponding to each peak in the fitness surface are reinforced and maintained by frequency dependent selection in conjunction with disruptive selection against intermediate strategies (Schluter and Nychka 1994, Smith and Skúlason 1996, Smith and Girman 2000, Benkman 2003).

Aside from the evolutionary significance of intraspecific variation (Futuma and Moreno 1988), 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. There are abundant examples of predator populations whose diet or foraging behavior change as a function of food abundance (e.g. Costa et al. 1989, Monaghan et al. 1994, Croxall et al. 1999, Metcalfe et al. 1999); however, the presence of alternative foraging strategies or specialist types may tend to mask or complicate these patterns. Declines in the relative abundance of a particular prey type will affect individuals to differing degrees depending on their diet specialization (e.g. Boag and Grant 1981); consequently, we might expect greater variability in foraging success (and thus greater variation in individual fitness) in a food-limited population of specialists than in a food-limited population of generalists. Age-, sex- and habitat-related differences in diet add further complexity to the predicted patterns of food limitation. Characterizing the sources of variation in diet – individual,

spatial and temporal – can help to clarify the relationships between foraging ecology and population dynamics (Partridge and Green 1985).

Aquatic, 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 previous studies have documented 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 has been found to increase 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).

I 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. I collected longitudinal, observational data from marked study animals over a 3 year period at two locations. Otter densities were relatively high and temporally stable (or decreasing slightly) at both locations, although the factors limiting population growth are unclear (Estes et al. 2003a). My objectives were threefold: first, I 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. Evidence from a prior long-term study of sea otters in Monterey Bay indicated a high degree of individual variation in diet (Estes et al. 2003b), but it is not clear whether this variation corresponded to distinct foraging modes. My 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, I wished to describe the interrelationships between foraging strategy and foraging

success. Specifically, I 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. Evidence for correlational selection on foraging behavior would be indicated by multiple peaks in the surface, and by interactive effects of behavioral variables on foraging success (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 as part of an ongoing population study of the southern sea otter (see Chapter 1). Sea otters were captured at three locations: Pt. Conception, (the southern periphery of the current range of the southern sea otter), San Simeon/Cambria (the south-central portion of the range), and Monterey Peninsula (the north-central portion of the range). Because very few foraging observations were obtained from animals at Pt. Conception, I limit consideration here to the latter two locations, referred to henceforth as Site 1 (San Simeon) and Site 2 (Monterey; Figure 2.1).

Capture and tagging activities were conducted intermittently throughout the study period, resulting in a gradually increasing sample size (Table 2.1). 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,

I 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 2.1).

I 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 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 5cm 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 I 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, I augmented the shore-based observations for these animals with boat-based observations, using a 17 foot skiff. In the case of boat-based observations I used 12× image-stabilized binoculars to view the otters, but all other methods were identical to shore-based observations.

Data Analysis

I 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. I used this index to evaluate spatial and temporal differences in diet

composition at the level of the population. To evaluate seasonal variation, I tested for an interaction between month and prey type. To evaluate spatial variation I 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, as well as 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 D). For each successful dive that was observed ($j=1,2,\dots,J$), 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). I calculated p_i , the proportion of the diet (in terms of biomass) comprised by prey type i , as:

$$p_i = \frac{\sum_j n_{i,j} m_{i,j}}{\sum_i \sum_j n_{i,j} m_{i,j}} \quad 30$$

Equation 30 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, I calculated a “proportional similarity” index (PS_k) for each otter:

$$PS_k = \sum_i \min \left(\frac{p_{i,k}}{\sum_i p_{i,k}}, \frac{\sum_k p_{i,k}}{\sum_k \sum_i p_{i,k}} \right) \quad 31$$

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). I 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. I 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. Previous reports of specialization in sea otters do not describe consistent dietary modes (Lyons 1991, Estes et al. 2003b), but these were based on smaller sample sizes and were not specifically testing for such patterns. In order to distinguish between the two alternate scenarios of individual variation described above, I used a combination of cluster analysis and discriminant analysis to test for consistent, distinct categories of diet composition.

To simplify interpretation of results, I combined similar prey species together to form 13 exhaustive prey categories (Table 2.2). 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 diet types represent the variables of interest. I 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). I used Wards 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, I 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. I compared *PSI* values among diet types using single-factor ANOVA, to determine whether the degree of prey specialization differed between diet types. I 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).

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 were measured. I 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 I 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).

I analyzed patterns of variation in the PCA factor scores to test for differences in foraging behavior attributable to study site, sex, and diet type. I 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). I 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. I 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, I repeated the PCA analysis described above, but used individual foraging bouts as the sample unit. I 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.

I 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) I 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 I 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 ($\text{kJ}\cdot\text{min}^{-1}$). 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 D) 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 2.2), 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 \geq 45s and < 90s; long ST \geq 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.

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), I 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). I calculated expected foraging effort based on the observed body weight and estimated rate of energy acquisition for each individual. I assumed that mean daily maintenance requirements were $1019 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$, the average of several published values for sea otters (Costa 1978, Costa and Kooyman 1982, Dean et al. 2002). I calculated the required total daily energy

input, and divided this by the estimated rate of energy gain to obtain the expected time budget. I 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. I evaluated the importance of foraging success to individual fitness by examining the relationship between rate of energy gain and female body condition. First, I 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). I 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, I 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 :

$$w_i = \frac{E_i}{\bar{E}} \quad 32$$

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). I 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, I 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 2.2). 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 2.3). 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 2.2).

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 2.3). The *PSI* score at site 2 (0.49) was slightly lower than site 1 (0.57), although this difference was not statistically significant (Table 2.3). 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 2.4). Individual otters were easily partitioned into the three diet groupings by discriminant analysis (Figure 2.5), and jack-knife re-sampling of the data resulted in correct group assignment 93% of the time (Appendix E). 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 2.6). The *PSI* scores differed between diet types (Table 2.3), 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).

Principle Component Analysis indicated that 87% of the individual variation in dive behavior could be explained by 3 factors (Appendix F). 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 F).

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 2.7). 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). I was unable to detect significant differences in Factor 3 between diet types ($F=0.306$, $P_{adj}=0.965$, power =

0.77), sexes ($F=0.756$, $P_{\text{adj}}=0.708$, power = 0.86) or study sites ($F=3.284$, $P_{\text{adj}}=0.179$, 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%).

The estimated mean rate of energy gain while foraging for all animals in the current study was $29.4 \text{ kJ}\cdot\text{min}^{-1}$, but this rate varied between individuals and also showed considerable variation from bout-to-bout (within-individual variance; Table 2.4). 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 2.4), 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 2.8).

The estimated rate of energy gain while foraging was a good predictor of female body condition (Figure 2.9), consistent with the hypothesized relationship between foraging

success and individual fitness. Based on the estimated energy requirements for maintenance metabolism, I 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 2.10).

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 2.11). 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 ($\gamma = 0.593$).

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, Kvittek 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 2.2). 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 2.3) 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 2.3). 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 2.3). Individual specialization is expected to become more pronounced as the degree of intra-specific 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 2.4 and Figure 2.5). It should be emphasized that the dietary characterizations of each diet type (Figure 2.6) 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 E). However, although kelp crabs and urchins occurred on a relatively high percentage of recorded foraging dives (Table 2.2), 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 2.4); however, based on the distribution of inter-cluster distances and on the unequivocal results of the discriminant analysis (Figure 2.5), I believe the three groups I 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 2.7). 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 2.4). 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 my analysis was derived from the published literature (Appendix D). 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 2.10) 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 2.9). The weight/length residuals were, without exception, negative for females whose rate of energy gain was below $20 \text{ kJ}\cdot\text{min}^{-1}$: interestingly, this value closely matches the predicted maintenance requirement of $19.6 \text{ kJ}\cdot\text{min}^{-1}$ 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 2.4). 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 2.8). 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 2.11). 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 2.11). 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.

Tables

Table 2.1 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 Site	Year	Study Animals Captured		Number of bouts observed	Number of dives recorded
		Females	Males		
1. San Simeon	2001	9	3	196	10778
	2002	18	5	209	10244
	2003	0	0	298	12231
	2004	0	0	24	937
	<i>sub-total:</i>	<i>27</i>	<i>8</i>	<i>727</i>	<i>34190</i>
2. Monterey	2001	5	1	25	1641
	2002	2	0	105	4484
	2003	14	3	113	5169
	2004	0	0	62	2568
	<i>sub-total:</i>	<i>21</i>	<i>4</i>	<i>305</i>	<i>13862</i>
Total:		48	12	1032	48052

Table 2.2. Summary of diet composition of sea otters at two study sites, showing the frequency of occurrence of prey types on foraging dives (prey comprising $\leq 0.1\%$ 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).

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

Table 2.3. 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, F = 3.93, P = 0.052, power = 0.86
Site 2	0.49	0.036	
Type 1 diet specialists	0.64	0.029	All pairwise comparisons significant, F = 17.57, P < 0.0001
Type 2 diet specialists	0.51	0.023	
Type 3 diet specialists	0.29	0.054	
All animals, current study	0.54	0.021	Significant difference, t = 2.47, P = 0.016
1980's study	0.68	0.032	

Table 2.4. Means and standard deviations in the estimated rate of energy acquisition while foraging ($\text{kJ}\cdot\text{min}^{-1}$) 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).

Demographic Group	Parameter	Site 1	Site 2	Both Sites	Prey specialization		
					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

Figures

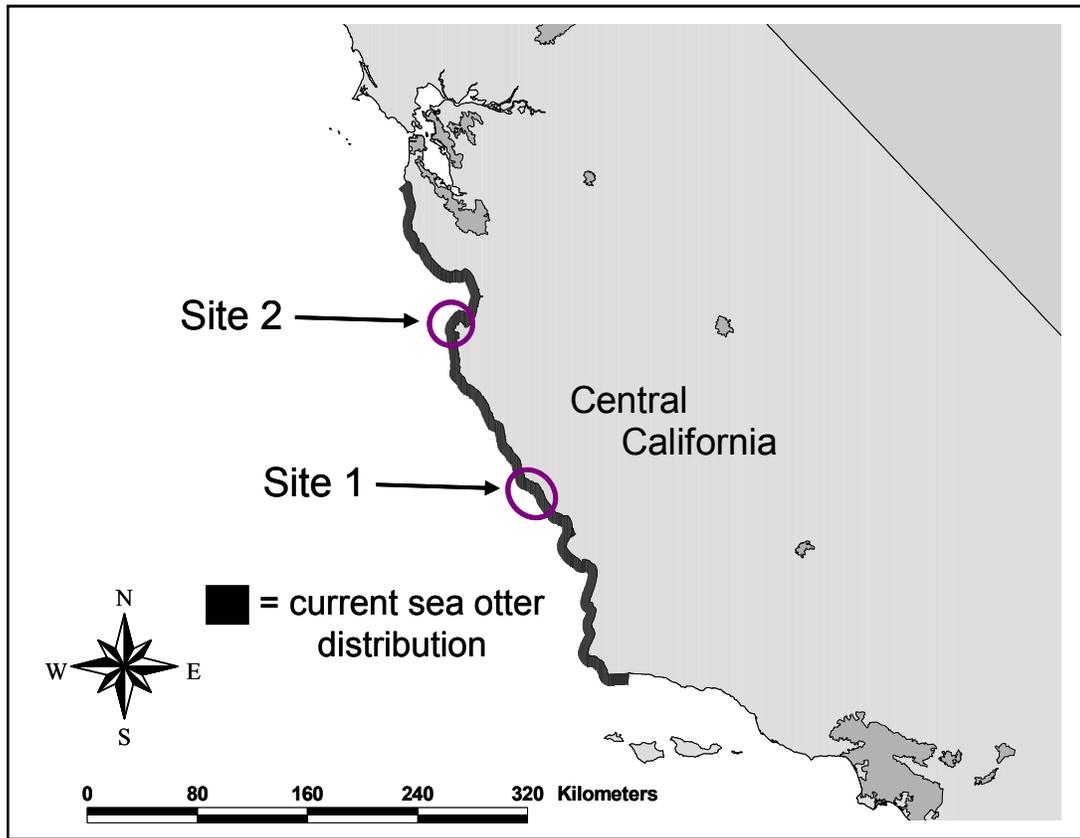


Figure 2.1 Map of the central California showing the current distribution of the sea otter (*Enhydra lutris nereis*) and the locations of the two study sites

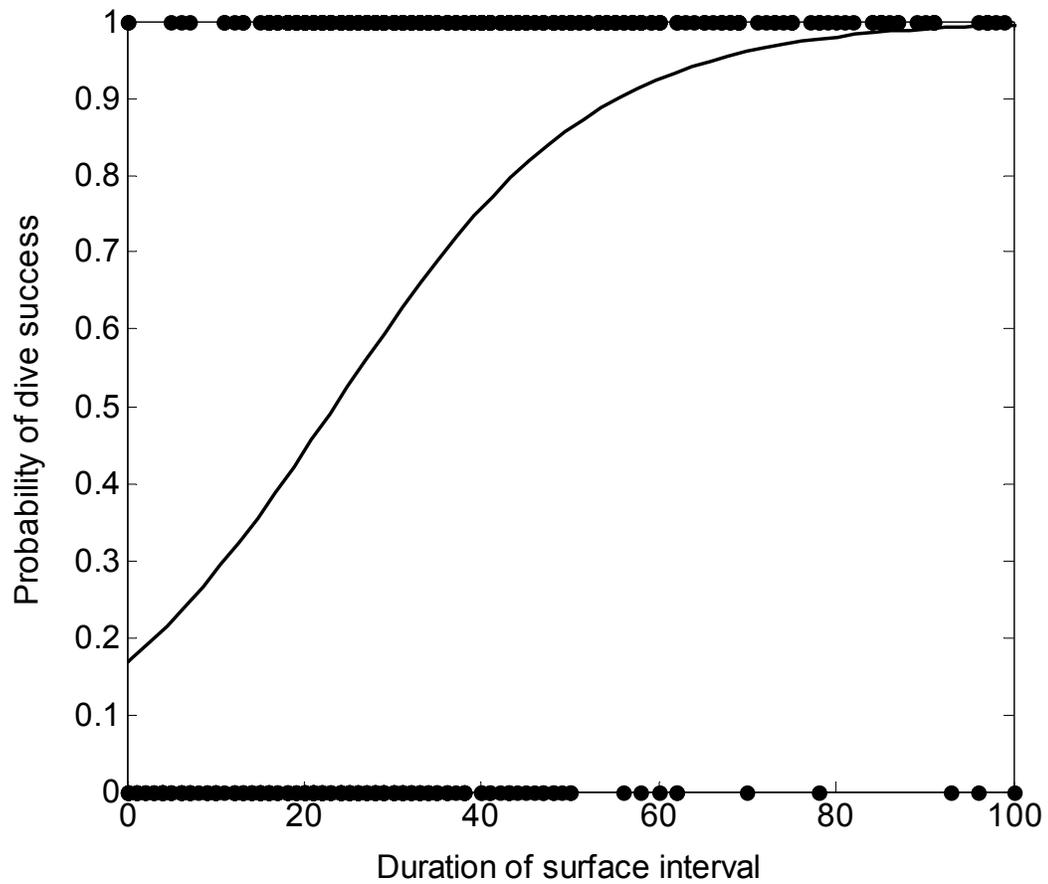


Figure 2.2 Sample data from one study animal illustrating the relationship between dive outcome (score of 1 = one or more prey items captured, 0 = no prey captured) and the duration of the post-dive surface interval. A logit function is fit to the data, and this function is then used to estimate the probability of dive success for dives in which the surface interval was recorded but the dive outcome was undetermined.

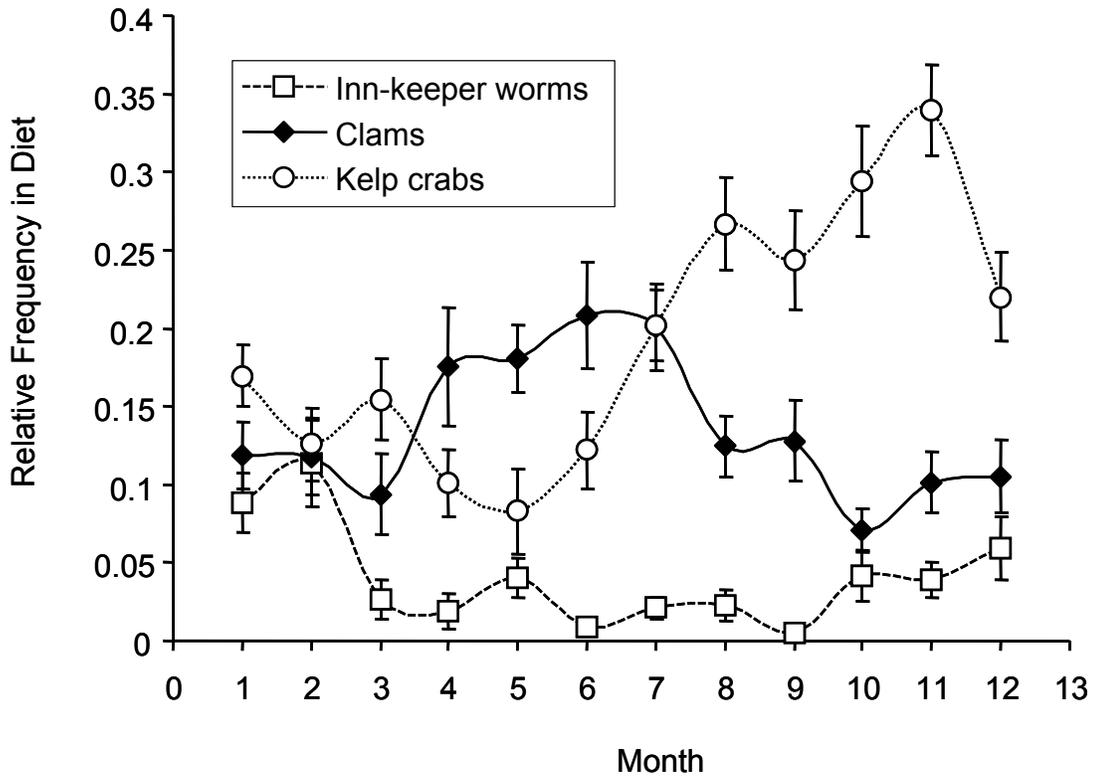


Figure 2.3 The relative frequency of occurrence (at the population-level) is shown for three prey types over the course of one year, illustrating patterns of seasonal variation observed in sea otter diets.

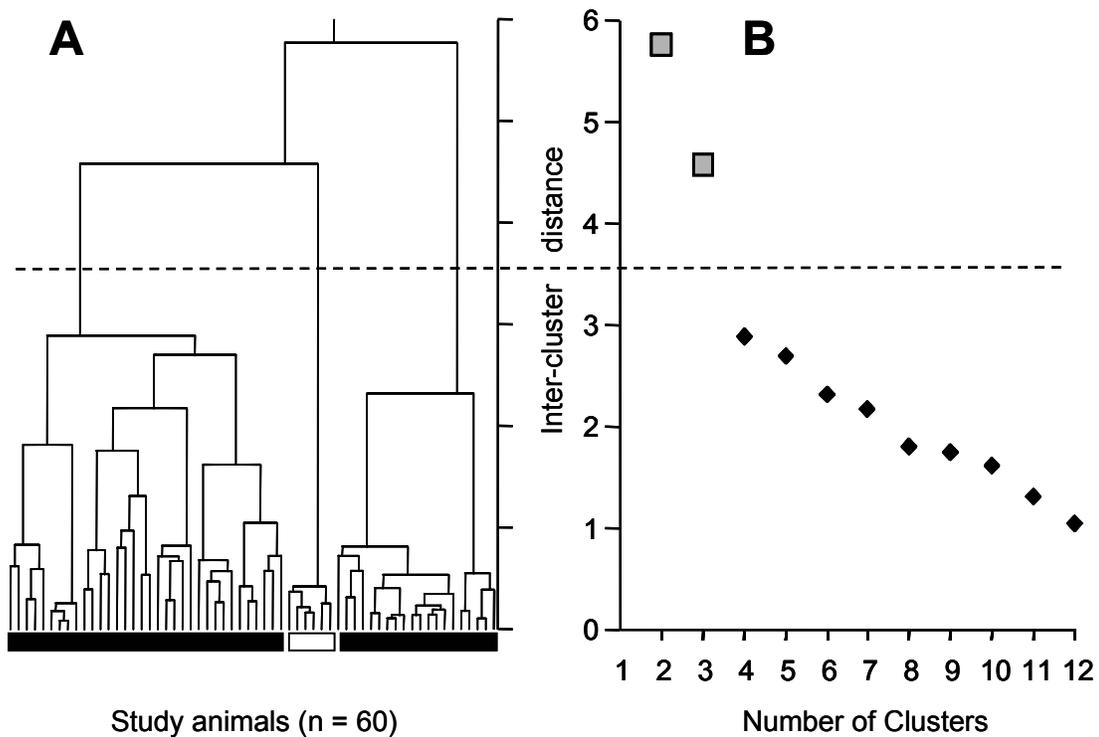


Figure 2.4 The results of a cluster analysis used to detect natural groupings of diet composition among individual sea otters (sample units) based on their consumption of 13 prey types. A) Dendrogram showing hierarchical relationships between sample units, with branch length indicating the relative distance 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.

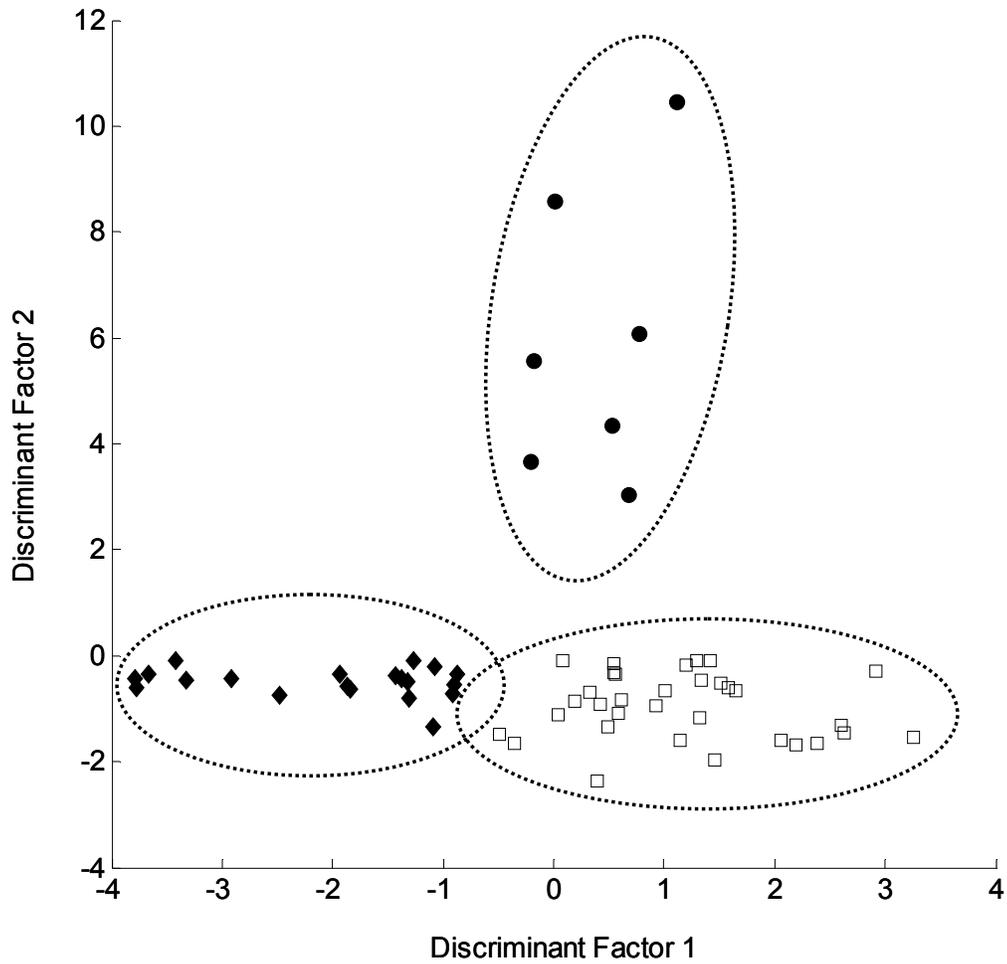


Figure 2.5 Discriminant Analysis scores are plotted for the two discriminant factors, which represent multivariate ordinations of 13 prey types. Data points represent individual otters, which have been classified by the cluster analysis into one of three groups based on their diet composition (type 1 = filled diamonds, type 2 = open squares, type 3 = filled circles). Diet types are well discriminated into distinct groupings along the two axes.

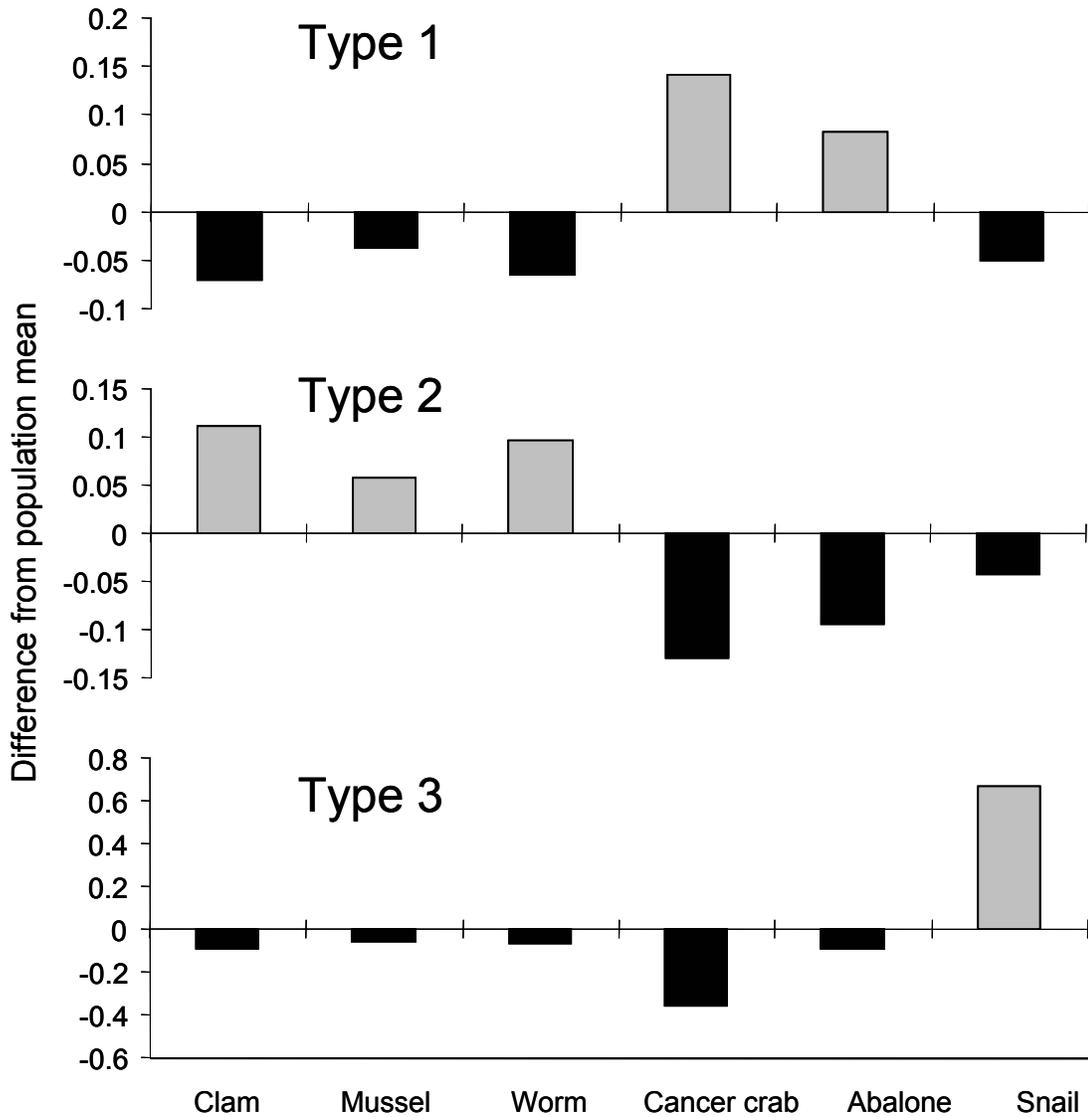


Figure 2.6 The relative frequency of six prey types are shown for the three types of diet specialist. Relative frequency was calculated as the proportion of the diet comprised by each prey type (in terms of wet edible biomass), and values were standardized by expressing them as differences from the population mean.

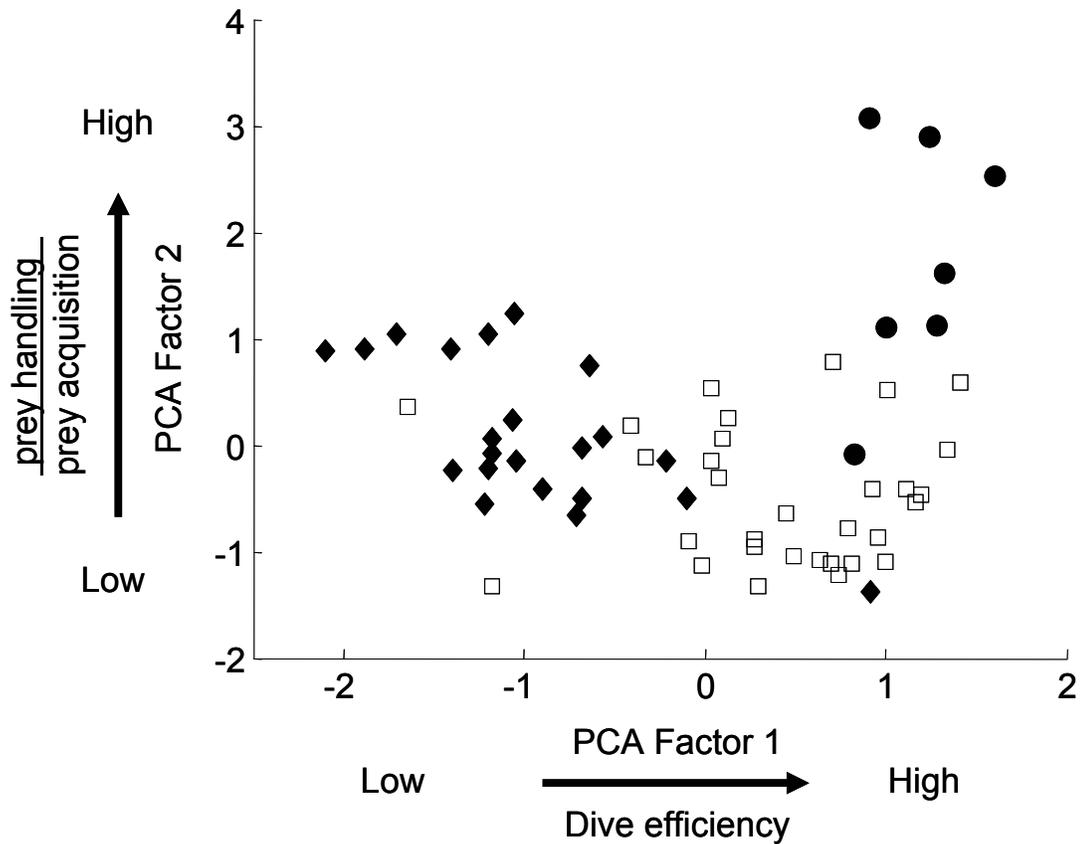


Figure 2.7 Factor scores are plotted for the first two ordination axes from a principal component analysis of foraging behavior. Data points represent individual otters, classified by diet composition (type 1 = filled diamonds, type 2 = open squares, type 3 = filled circles). Factor 1 represents an axis 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.

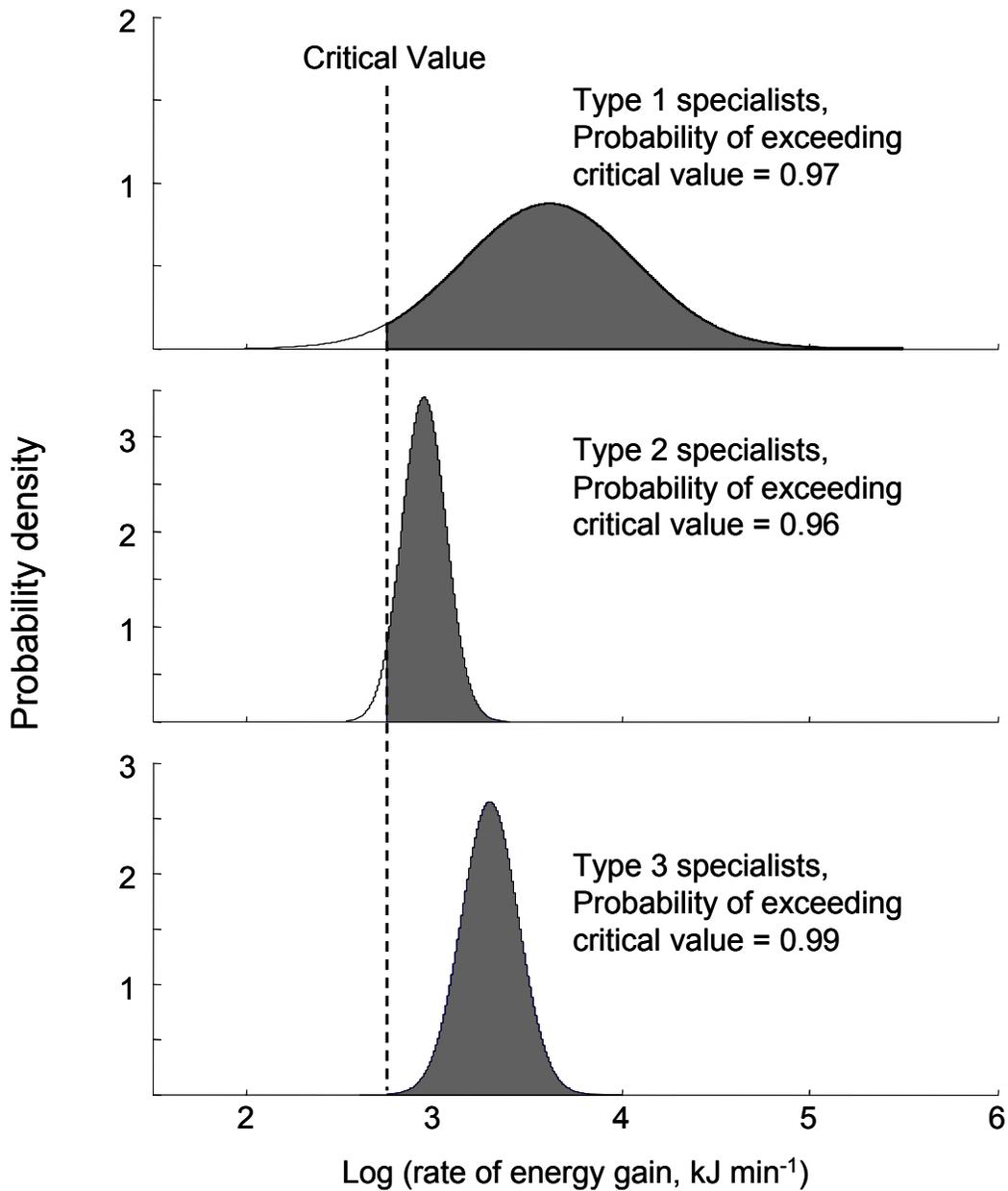


Figure 2.8 Probability density functions of the rate of energy gain for female otters (with large pups), plotted separately for individuals of each prey specialization type. The vertical dashed line represents an arbitrary “critical value”, calculated as 90% of the average rate that would be required 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.

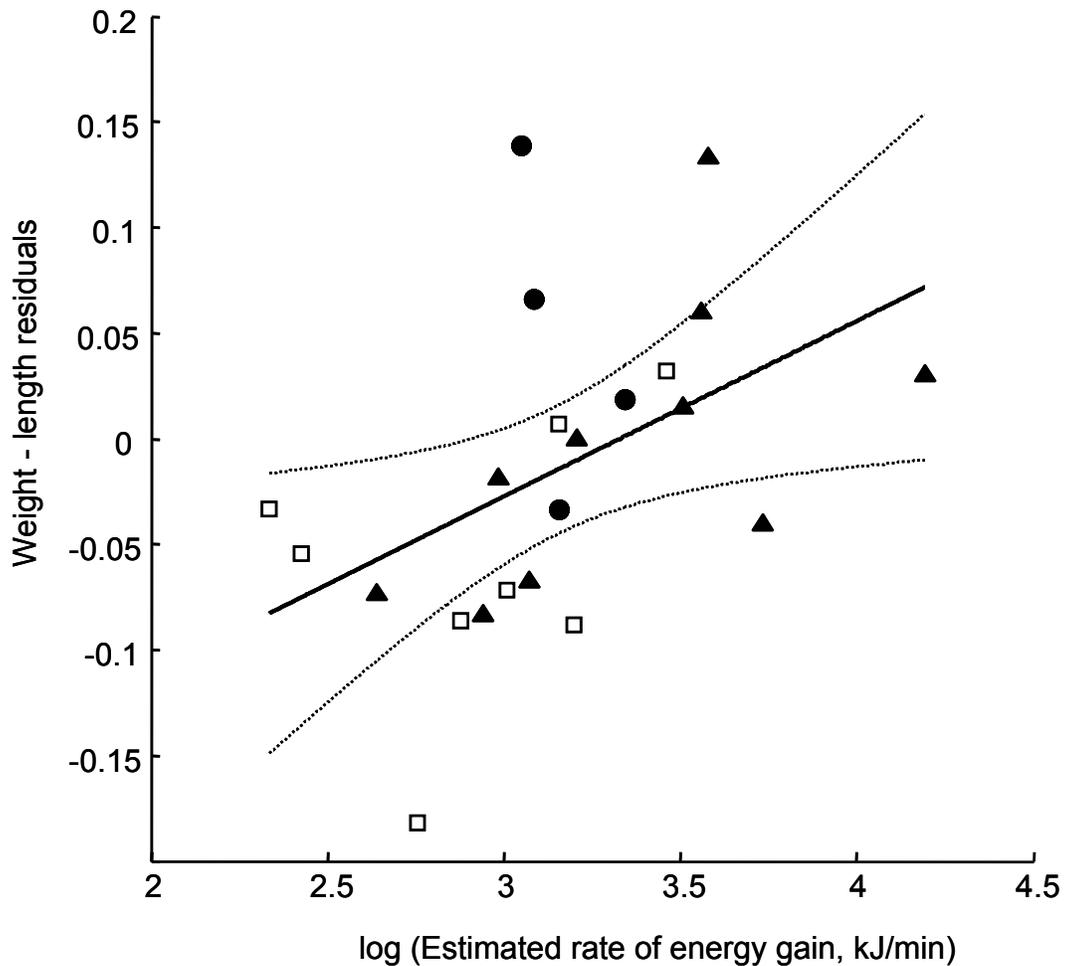


Figure 2.9. Weight-length residuals for adult female study animals plotted against the estimated rate of energy gain while foraging (log-transformed). Individual otters are classified by their diet specialization: type 1 = filled diamonds, type 2 = open squares, type 3 = filled circles. The solid line 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.

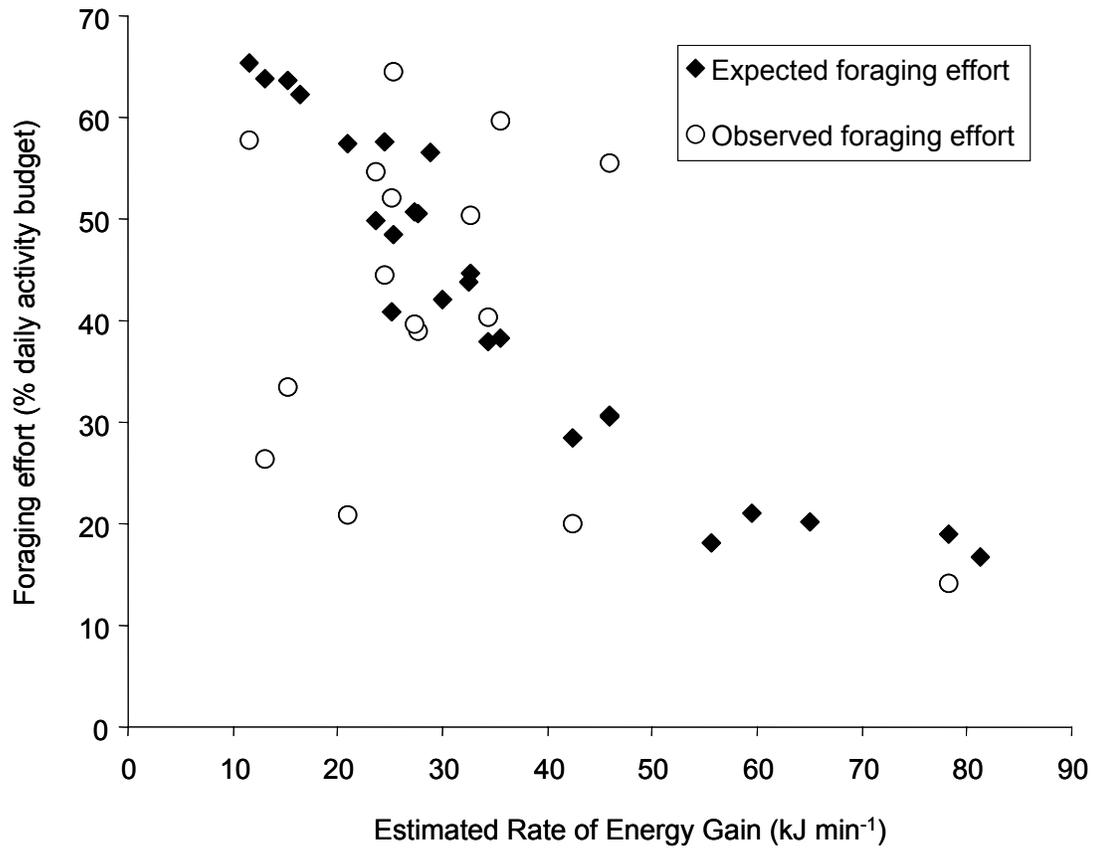


Figure 2.10 Foraging effort (percent of time spent foraging) plotted against estimated rate of energy gain while foraging. Expected values (filled diamonds) were calculated based on the amount of foraging time that would be needed to meet maintenance requirements, accounting for body weight. Actual percent 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.

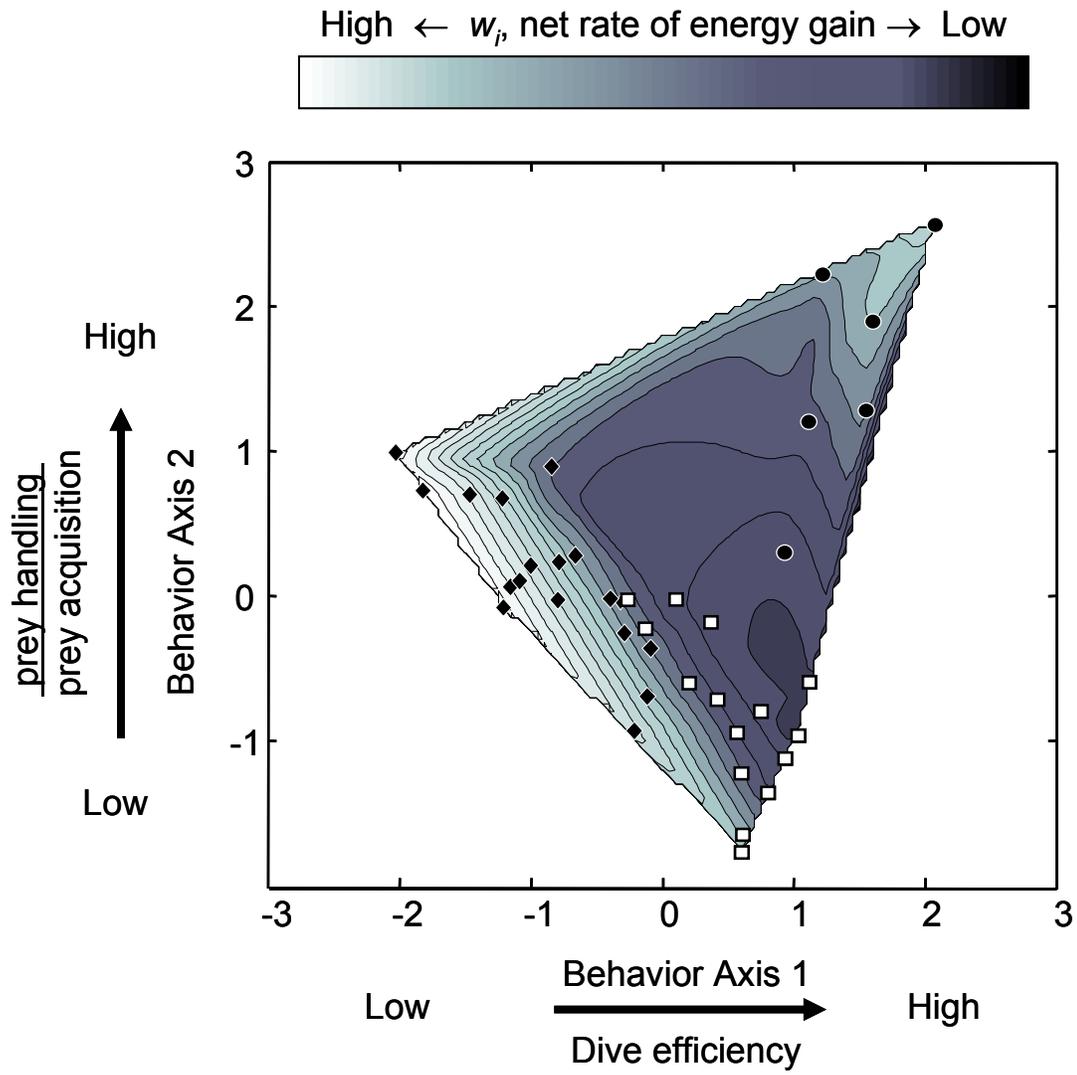


Figure 2.11 An ordination of the first two principal components of foraging behavior, with a fitness surface superimposed as a contour map: contour elevation corresponds to the net rate of energy gain, w_i . The fitness surface was calculated using a multivariate cubic spline algorithm (see text for explanation), and the smoothing factor used ($\lambda = -0.9$) 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.

References

- Abrams, P. A. 1993. Optimal traits when there are several costs: The interaction of mortality and energy costs in determining foraging behavior. *Behavioral Ecology* **4**:246-253.
- Adams, N. J., R. W. Abrams, W. R. Siegfried, K. A. Nagy, and I. R. Kaplan. 1991. Energy expenditure and food consumption by breeding cape gannets *Morus capensis*. *Marine Ecology Progress Series* **70**:1-9.
- Bacon, C. E., W. M. Jarman, J. A. Estes, M. Simon, and R. J. Norstrom. 1999. Comparison of organochlorine contaminants among sea otter (*Enhydra lutris*) populations in California and Alaska. *Environmental Toxicology and Chemistry* **18**:452-458.
- Ball, J. P. 1994. Prey choice of omnivorous canvasbacks: Imperfectly optimal ducks? *Oikos* **70**:233-244.
- Barbosa, A., M. Barluenga, and E. Moreno. 2000. Effects of body mass on the foraging behaviour of subordinate Coal Tits *Parus ater*. *Ibis* **142**:428-434.
- Barkan, C. P. L. 1990. A field test of risk-sensitive foraging in black-capped chickadees (*Parus atricapillus*). *Ecology (Tempe)* **71**:391-400.
- Beauchamp, G., L. A. Giraldeau, and N. Ennis. 1997. Experimental evidence for the maintenance of foraging specializations by frequency-dependent choice in flocks of spice finches. *Ethology Ecology & Evolution* **9**:105-117.
- Benkman, C. W. 1993. Adaptation to single resources and the evolution of crossbill (*Loxia*) diversity. *Ecological Monographs* **63**:305-325.
- Benkman, C. W. 2003. Divergent selection drives the adaptive radiation of crossbills. *Evolution* **57**:1176-1181.
- Boag, P. T., and P. R. Grant. 1981. Intense natural selection on a population of Darwin's finches (*Geospizinae*) in the Galapagos. *Science* **214**:82-85.
- Bodkin, J. L., A. M. Burdin, and D. A. Ryazanov. 2000. Age- and sex-specific mortality and population structure in sea otters. *Marine Mammal Science* **16**:201-219.
- Bolnick, D. I., R. Svanback, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist* **161**:1-28.
- Bolnick, D. I., L. H. Yang, J. A. Fordyce, J. M. Davis, and R. Svanback. 2002. Measuring individual-level resource specialization. *Ecology* **83**:2936-2941.

- Boyd, I. L., D. J. McCafferty, and T. R. Walker. 1997. Variation in foraging effort by lactating Antarctic fur seals: Response to simulated increased foraging costs. *Behavioral Ecology and Sociobiology* **40**:135-144.
- Caraco, T., and R. G. Gillespie. 1986. Risk-sensitivity: Foraging mode in an ambush predator. *Ecology (Tempe)* **67**:1180-1185.
- Carroll, J. C. 1982. Seasonal Abundance Size Composition and Growth of Rock Crab *Cancer-Antennarius* Off Central California USA. *Journal of Crustacean Biology* **2**:549-561.
- Clark, A. B., and T. J. Ehlinger. 1973. Pattern and adaptation in individual behavioral differences. Pages 1-47 *in* P. P. G. Bateson and P. H. Klopfer, editors. *Perspectives in Ethology*. Plenum Publishing Corp., New York, NY.
- Clark, C., and M. Mangel. 2000. *Dynamic state variable models in ecology: methods and applications*. Oxford University Press, New York, NY.
- Clarke, J., B. Manly, K. Kerry, H. Gardner, E. Franchi, S. Corsolini, and S. Focardi. 1998. Sex differences in Adelie penguin foraging strategies. *Polar Biology* **20**:248-258.
- Cohen, J. 1988. *Statistical power analysis for the behavioral sciences*, 2nd edition. L. Erlbaum Associates, Hillsdale, N.J.
- 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.
- Costa, D. P. 1988. Methods for studying the energetics of freely diving mammals. *Canadian Journal of Zoology* **66**:45-52.
- Costa, D. P., J. P. Croxall, and C. D. Duck. 1989. Foraging energetics of antarctic fur seals in relation to changes in prey availability. *Ecology (Tempe)* **70**:596-606.
- Costa, D. P., and G. L. Kooyman. 1982. Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. *Canadian Journal of Zoology* **60**:2761-2767.
- Craven, P., and G. Wahba. 1978. Smoothing noisy data with spline functions: estimating the correct degree of smoothing by the method of generalized cross-validation. *Numerische Mathematik* **31**:377--403.
- Croll, D. A., and E. McLaren. 1993. Diving metabolism and thermoregulation in common and thick-billed murre. *Journal of Comparative Physiology B* **163**:160-166.
- Croxall, J. P., R. W. Davis, and M. J. O'Connell. 1988. Diving Patterns in Relation To Diet of Gentoo and Macaroni Penguins at South Georgia Usa. *Condor* **90**:157-167.

- Croxall, J. P., K. Reid, and P. A. Prince. 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology Progress Series* **177**:115-131.
- Dean, T. A., J. L. Bodkin, A. K. Fukuyama, S. C. Jewett, D. H. Monson, C. E. O'Clair, and G. R. VanBlaricom. 2002. Food limitation and the recovery of sea otters following the 'Exxon Valdez' oil spill. *Marine Ecology-Progress Series* **241**:255-270.
- Doidge, D. W., and J. P. Croxall. 1989. Factors affecting weaning weight in Antarctic fur seals *Arctocephalus gazella* at South Georgia [Antarctica]. *Polar Biology* **9**:155-160.
- Doroff, A. M., and A. R. Degange. 1994. Sea otter, *Enhydra lutris*, prey composition and foraging success in the northern Kodiak Archipelago. *U S National Marine Fisheries Service Fishery Bulletin* **92**:704-710.
- Ebert, E. E. 1968. A food habits study of the southern sea otter, *Enhydra lutris nereis*. *California Fish and Game* **54**:33-42.
- Ehlinger, T. J. 1990. Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. *Ecology* **71**:886-896.
- Emlen, J. M. 1966. The role of time and energy in food preference. *American Naturalist* **100**:611-617.
- Endler, J. A. 1986. *Natural selection in the wild*. Princeton University Press, Princeton, NJ.
- Estes, J. A. 1990. Growth and equilibrium in sea otter populations. *Journal of Animal Ecology* **59**:385-402.
- Estes, J. A., B. B. Hatfield, K. Ralls, and J. Ames. 2003a. Causes of mortality in California sea otters during periods of population growth and decline. *Marine Mammal Science* **19**:198-216.
- Estes, J. A., R. J. Jameson, and A. M. Johnson. 1981. Food selection and some foraging tactics of sea otters. Pages 606-641 *in* J. A. Chapman and D. Pursley, editors. *Worldwide Furbearer Conference Proceedings, Volume 1*. University of Maryland Press, Baltimore, Maryland.
- Estes, J. A., R. J. Jameson, and E. B. Rhode. 1982. Activity and prey selection in the sea otter: influence of population status on community structure. *American Naturalist* **120**:242-258.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* **185**:1058-1060.

- Estes, J. A., M. L. Riedman, M. M. Staedler, M. T. Tinker, and B. E. Lyon. 2003b. Individual variation in prey selection by sea otters: patterns, causes and implications. *Journal of Animal Ecology* **72**:144-155.
- Estes, J. A., K. E. Underwood, and M. J. Karmann. 1986. Activity-time budgets of sea otters in California. *Journal of Wildlife Management* **50**:626-636.
- 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.
- Feinsinger, P., E. E. Spears, and R. W. Poole. 1981. A simple measure of niche breadth. *Ecology* **62**:27-32.
- Futuma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. *Annual Review of Systematics and Ecology* **19**:207-233.
- Garshelis, D. L., J. A. Garshellis, and A. T. Kimker. 1986. Sea otter time budgets and prey relationships in Alaska. *Journal of Wildlife Management* **50**:637-647.
- Gauch, H. G. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, Cambridge, UK.
- Gelatt, T. S., D. B. Siniff, and J. A. Estes. 2002. Activity patterns and time budgets of the declining sea otter population at Amchitka Island, Alaska. *Journal of Wildlife Management* **66**:29-39.
- Gentry, R. L., D. P. Costa, J. P. Croxall, J. H. M. David, R. W. Davis, G. L. Kooyman, P. Majluf, T. S. McCann, and F. Trillmich. 1986. Synthesis and conclusions. Pages 220-264 *in* R. L. Gentry and G. L. Kooyman, editors. *Fur Seals: Maternal Strategies on Land and at Sea*. Princeton University Press, Princeton, N.J.
- Gillespie, R. G., and T. Caraco. 1987. Risk-sensitive foraging strategies of two spider populations. *Ecology (Tempe)* **68**:887-899.
- Glasser, J. W. 1982. A theory of trophic strategies: the evolution of facultative specialists. *American Naturalist* **119**:250-262.
- Green, A. J. 2001. Mass/length residuals: Measures of body condition or generators of spurious results? *Ecology* **82**:1473-1483.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, NJ.
- Hughes, R. N. 1979. Optimal diets under the energy maximization premise: The effects of recognition time and learning. *American Naturalist* **113**:209-222.

- 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.
- Kacelnik, A., and M. Bateson. 1996. Risky theories: The effects of variance on foraging decisions. *American Zoologist* **36**:402-434.
- Kreuder, C., M. A. Miller, D. A. Jessup, L. J. Lowenstine, M. D. Harris, J. A. Ames, T. E. Carpenter, P. A. Conrad, and J. A. K. Mazet. 2003. Patterns of mortality in southern sea otters (*Enhydra lutris nereis*) from 1998-2001. *Journal of Wildlife Diseases* **39**:495-509.
- Kruuk, H., and A. Moorhouse. 1990. Seasonal and spatial differences in food selection by otters (*Lutra lutra*) in Shetland (Scotland, UK). *Journal of Zoology (London)* **221**:621-638.
- Kvitek, R. G., C. E. Bowlby, and M. Staedler. 1993. Diet and foraging behavior of sea otters in southeast Alaska. *Marine Mammal Science* **9**:168-181.
- Kvitek, R. G., and J. S. Oliver. 1988. Sea Otter Foraging Habits and Effects on Prey Populations and Communities in Soft-Bottom Environments. *in* G. R. Vanblaricom and J. A. Estes, editors. *The Community Ecology of Sea Otters*. Springer Verlag Inc., New York.
- Loughlin, T. R., J. L. Bengston, and R. L. Merrick. 1987. Characteristics of feeding trips of female northern fur seals. *Canadian Journal of Zoology* **65**:2079-2084.
- Lyons, K. J. 1991. Variation in feeding behavior of female sea otters, *Enhydra lutris*, between individuals and with reproductive condition. Ph.D. dissertation. University of California, Santa Cruz, Santa Cruz, CA.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* **100**:603-609.
- Mangel, M., and C. Clark. 1988. *Dynamic modeling in behavioral ecology*. Princeton University Press, Princeton, N.J.
- Mathews, C. R. 1996. Diet Profitability for the California Sea Otter, *Enhydra lutris*. Masters dissertation. University of California, Santa Cruz, Santa Cruz, CA.
- McCleneghan, K., and J. A. Ames. 1976. A unique method of prey capture by the sea otter, *Enhydra lutris* Linnaeus. *Journal of Mammalogy* **57**:410-412.
- McGarigal, K., S. Cushman, and S. Stafford. 2000. *Multivariate statistics for wildlife and ecology research*. Springer-Verlag, New York, NY.

- McNamara, J. M., and A. I. Houston. 1992. Risk-Sensitive Foraging A Review of the Theory. *Bulletin of Mathematical Biology* **54**:355-378.
- Metcalfe, N. B., N. H. C. Fraser, and M. D. Burns. 1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *Journal of Animal Ecology* **68**:371-381.
- Miller, M. A., I. A. Gardner, C. Kreuder, D. M. Paradies, K. R. Worcester, D. A. Jessup, E. Dodd, M. D. Harris, J. A. Ames, A. E. Packham, and P. A. Conrad. 2002. Coastal freshwater runoff is a risk factor for *Toxoplasma gondii* infection of southern sea otters (*Enhydra lutris nereis*). *International Journal for Parasitology* **32**:997-1006.
- Monaghan, P., P. Walton, S. Wanless, J. D. Uttley, and M. D. Burns. 1994. Effects of prey abundance on the foraging behavior, diving efficiency and time allocation of breeding guillemots *Uria aalge*. *Ibis* **136**:214-222.
- Monson, D. H., J. A. Estes, J. L. Bodkin, and D. B. Siniff. 2000. Life history plasticity and population regulation in sea otters. *Oikos* **90**:457-468.
- Monson, D. H., C. McCormick, and B. E. Ballachey. 2001. Chemical anesthesia of northern sea otters (*Enhydra lutris*): results of past field studies. *Journal of Zoo & Wildlife Medicine* **32**:181-189.
- Mori, Y. 1998. Optimal choice of foraging depth in divers. *Journal of Zoology; proceedings of the Zoological Society of London* **245**:279-283.
- Neter, J., W. Wasserman, and M. H. Kutner. 1990. *Applied Linear Statistical Models: Regression, Analysis of Variance, and Experimental Designs*, 3rd edition. Irwin, Chicago.
- Ostfeld, R. S. 1982. Foraging strategies and prey switching in the California sea otter. *Oecologia* **53**:170-178.
- Partridge, L., and P. Green. 1985. Intraspecific feeding specializations and population dynamics. Pages 207-226 *in* R. M. Sibley and R. H. Smith, editors. *Behavioral Ecology*. Blackwell Press, Oxford, UK.
- Pierotti, R., and C. A. Annett. 1991. Diet Choice in the Herring Gull Constraints Imposed by Reproductive and Ecological Factors. *Ecology* **72**:319-328.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology* **52**:137-154.
- Ralls, K., B. B. Hatfield, and D. B. Siniff. 1995. Foraging patterns of California sea otters as indicated by telemetry. *Canadian Journal of Zoology* **73**:523-531.

- Ralls, K., and D. B. Siniff. 1990. Time budgets and activity patterns in California sea otters. *Journal of Wildlife Management* **54**:251-259.
- Real, L., and T. Caraco. 1986. Risk and foraging in stochastic environments. *Annual Review of Ecology and Systematics* **17**:371-390.
- Reinhardt, U. G., and M. C. Healey. 1999. Season- and size-dependent risk taking in juvenile coho salmon: Experimental evaluation of asset protection. *Animal Behaviour* **57**:923-933.
- Riedman, M. L., and J. A. Estes. 1990. The Sea Otter *Enhydra-Lutris* Behavior Ecology and Natural History. U S Fish and Wildlife Service Biological Report **90**:I-III, 1-126.
- Schindler, D., J. R. Hodgson, and J. F. Kitchell. 1997. Density-dependent changes in individual foraging specialization of largemouth bass. *Oecologia (Berlin)* **110**:592-600.
- Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. *Evolution* **42**:849-861.
- Schluter, D., and D. Nychka. 1994. Exploring fitness surfaces. *American Naturalist* **143**:597-616.
- Silva, M. 1998. Allometric scaling of body length: Elastic or geometric similarity in mammalian design. *Journal of Mammalogy* **79**:20-32.
- Sinervo, B. 2000. Adaptation, natural selection and optimal life-history allocation in the face of genetically based trade-offs. Pages 41-64 *in* T. A. Mousseau, B. Sinervo, and J. A. Endler, editors. *Adaptive genetic variation in the wild*. Oxford University Press, New York, NY.
- Sinervo, B., and E. Svensson. 2002. Correlational selection and the evolution of genomic architecture. *Heredity* **89**:329-338.
- Skúlason, S., and T. B. Smith. 1995. Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution* **10**:366-370.
- Smith, T. B. 1987. Bill size polymorphism and intraspecific niche utilization in an African finch. *Nature* **329**:717-719.
- Smith, T. B., and D. J. Girman. 2000. Reaching new adaptive peaks. Pages 139-156 *in* T. A. Mousseau, B. Sinervo, and J. A. Endler, editors. *Adaptive genetic variation in the wild*. Oxford University Press, New York, NY.
- Smith, T. B., and S. Skúlason. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians and birds. *Annual Review of Systematics and Ecology* **27**:111-133.

- Sutherland, W. J., B. J. Ens, J. D. Goss-Custard, and J. B. Hulscher. 1996. Specialization. Pages 56-76 in J. D. Goss-Custard, editor. *The oystercatcher: From individuals to populations*. Oxford University Press, Inc., Oxford, England.
- Tanaka, K. 1991. Food consumption and diet composition of the web-building spider *Agelena limbata* in two habitats. *Oecologia (Berlin)* **86**:8-15.
- Wanless, S., M. P. Harris, and J. A. Morris. 1995. Factors affecting daily activity budgets of South Georgian shags during chick rearing at bird Island, South Georgia. *Condor* **97**:550-558.
- Watt, J., D. B. Siniff, and J. A. Estes. 2000. Inter-decadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska. *Oecologia (Berlin)* **124**:289-298.
- Werner, E. E., G. G. Mittelbach, and D. J. Hall. 1981. The Role of Foraging Profitability and Experience in Habitat Use by the Bluegill Sunfish. *Ecology* **62**:116-125.
- Werner, T. K., and T. W. Sherry. 1987. Behavioral feeding specialization in *Pinaroloxias inornata*, the "Darwin's Finch" of Cocos Island, Costa Rica. *Proceedings of the National Academy of Sciences of the United States of America* **84**:5506-5510.
- West, L. 1986. Interindividual variation in prey selection by the snail *Nucella emarginata*. *Ecology (Tempe)* **67**:798-809.
- West, L. 1988. Prey selection by the tropical snail *Thais melones*: A study of interindividual variation. *Ecology (Tempe)* **69**:1839-1854.
- Williams, T., and D. B. Siniff. 1983. Surgical implantation of radio telemetry devices in the sea otter. *Journal of the American Veterinary Medical Association* **11**:1290-1291.
- Wilson, R. P., B. M. Culik, G. Peters, and R. Bannasch. 1996. Diving behaviour of Gentoo penguins, *Pygoscelis papua*; factors keeping dive profiles in shape. *Marine Biology Berlin* **126**:153-162.

Chapter 3. Intra-specific variation in foraging specializations: modeling the effects of frequency dependence, learning, cultural transmission, and environmental variation

Introduction

Behavioral strategies – mate acquisition, parental care, foraging – are often described as fixed characteristics of animal species or populations, yet it is generally acknowledged that individuals within a population will display some level of variability in almost any behavioral trait that can be measured. Even experimental confirmations of the predictions of optimality theory often show that individuals differ significantly with respect to the behavior under study (e.g. Krebs et al. 1977). Individual foraging specializations have been recognized for many years (Clark and Ehlinger 1973, Heinrich 1979, West 1986, Werner and Sherry 1987, Bridcut and Giller 1995, Beauchamp et al. 1997, Schindler et al. 1997), as has the potential significance of foraging specializations from the perspectives of both evolutionary ecology and community-level processes (Roughgarden 1972, Chesson 1984, Futuyma and Moreno 1988, Hori 1993, Sherratt and MacDougall 1995). Bolnick et al. (2003) recently summarized the many previously published examples of individual foraging specializations, making a strong case that such individual variation is likely a widespread and important phenomenon. Yet despite evidence for the ubiquity of individual variation in foraging strategies, and recognition of the need to incorporate such variation into broader ecological theory (e.g. Sherratt and MacDougall 1995, Bolnick et al. 2003, Estes et al. 2003), there is as yet no quantitative model for understanding or predicting the dynamics of

alternative specializations. Here, I present a generalized theoretical framework for exploring individual foraging specializations.

I start with the simple and well supported observation that foraging specialists may be favored over generalists in cases where specialization results in higher detection rates, capture success, improved handling efficiency, or improved digestive efficiency (e.g. Clark and Ehlinger 1973, Heinrich 1976, Partridge 1976, Werner et al. 1981, Partridge and Green 1985, Werner and Sherry 1987, Mangel and Clark 1988, West 1988, Dukas and Clark 1995, Chittka and Thomson 1997, Kandori and Ohsaki 1998, Goulson 1999, Golet et al. 2000). One or more of these effects can occur as a result of a high degree of specificity of prey capture/handling skills (skills for one prey type cannot be transferred to other, dissimilar types) coupled with an inability to retain skills for multiple prey types (Hughes and O'Brien 2001). When prey-specific foraging skills are dynamic rather than fixed – that is to say, they can be learned or improved through practice, and likewise be lost through lack of practice or interference – then the decision of an individual to specialize rather than generalize, or to switch from one specialization to another, becomes a function of the particular foraging history of that individual, mediated by species-specific characteristics of learning and memory (Partridge 1976). Hughes (1979) demonstrated that the precise nature of the learning effect (i.e. the maximum possible improvement in foraging efficiency and the speed of learning and forgetting) could have important implications for the relative frequency of specialists and the likelihood of prey switching. However, because learning is inherently a dynamic process, in which individuals at any given time will behave according to their current state and past experience, a dynamic approach is needed to fully explore the effects of learning on foraging specializations (McNamara and Houston 1985, Houston and

McNamara 1988, Mangel and Clark 1988). Hughes' (1979) static model is of limited use in this regard, and also fails to explain the co-occurrence of alternative foraging specializations within a population.

The co-existence of alternative specializations is somewhat perplexing, as one would expect that selection against sub-optimal foraging specializations is relatively strong. Co-existence therefore requires some mechanism for diversification into multiple specialist types, two or more of which are able to coexist (at an ecological time scale) within the same population. A variety of selective and non-selective mechanisms have been proposed that may act alone or in concert to maintain alternative strategies (e.g. Clark and Ehlinger 1973, Houston and McNamara 1985, Partridge and Green 1985, Beauchamp et al. 1997, Schmitz et al. 1998). In a recently reported case study of prey specialization in southern sea otters (*Enhydra lutris nereis*), Estes et al. (2003) presented evidence for matrilineal transmission of foraging specializations, apparently resulting from pups learning prey-specific handling skills from their mothers. In sea otters, and perhaps in other species (Bonner 1980, Partridge and Green 1985), cultural transmission could potentially contribute to the maintenance of alternative strategies (Estes et al. 2003). Note that I am employing a very broad definition of cultural transmission as “information or behavior acquired from conspecifics through some form of social learning” (Bonner 1980, Boyd and Richerson 1996), and I am considering only the transmission of foraging skills (but see Rendell and Whitehead 2001).

Transmission of prey specializations from mother to offspring, and/or the horizontal transmission of learned skills between con-specifics, has been reported for a variety of taxa including primates (Huffman and Quiatt 1986, Lefebvre 1995, Stoinski et al. 2000), cetaceans (Heimlich-Boran 1988, Weinrich et al. 1992, Rendell and Whitehead 2001, Mann

and Sargeant 2003), sea birds (Norton-Griffiths 1968, Annett and Pierotti 1999), rodents (Terkel 1996) and mustelids (Estes et al. 2003). Aside from the individual examples mentioned above, however, little attention has been given to the potential role of cultural transmission as a driver of intra-specific variation in foraging behavior.

My goal is to develop a quantitative, conceptual framework that allows me to explore foraging specializations at two levels: first, at the individual level I seek to understand how and when the ability to modify skills through learning should affect an animal's decision to behave as a prey specialist or generalist; second, at the population level I seek to understand how particular behavioral and life-history characteristics of the forager and its prey populations will interact to mediate the co-occurrence of alternative foraging specializations. I pose three general questions about variation in foraging specializations: first, how does the ability to improve skills through learning affect a forager's propensity to specialize or generalize, and what other factors (including the temporal dynamics of the learning processes itself) are important in modifying this decision? Second, what characteristics of predator physiology, life history, behavior, and predator-prey interactions are important in determining the coexistence and relative frequency of alternative specialists, and the temporal dynamics of specializations within a population? Third, to what extent does cultural transmission mediate the relative frequencies of alternative specializations, and temporal variation in these frequencies?

Methods

General Approach

I develop two complementary models with which to achieve my objectives: I use a stochastic dynamic programming model (SDPM) to investigate the dynamics of an individual's predicted decision to specialize or generalize, and I use an individual based model (IBM) to investigate the population level dynamics of foraging specializations. Both of these models share the same basic assumptions about behavioral constraints, prey characteristics, and state variable dynamics. I begin with a simple prey selection model (Stephens and Krebs 1986) composed of sequential encounters between a forager and $i = 1$ to n potential prey types. At each time interval of searching ($t = 1, 2 \dots T$), I assume that a forager might encounter no prey (in which case it will resume searching during the subsequent interval), or it might encounter a maximum of one prey item. When a prey item is encountered, the forager may capture, handle and consume that prey item (which requires one or more additional time intervals) or resume searching for other prey. I further assume that each prey type is uniquely defined by the energy gained by consuming one item (g_i), its encounter rate (λ_i), and its baseline handling time (H_i). I distinguish "baseline" handling time from realized handling time (h_i), which can vary with the past experience or current state of the forager (see below). The likelihood of encountering no prey items after searching for a single time interval is given by $1 - \sum \lambda_i$; if prey is encountered, the likelihood that the item encountered belongs to prey type i is $\lambda_i / \sum \lambda_i$.

The dynamic state variables of interest to me are the forager's energy reserves and the forager's skills associated with each potential prey type. The state dynamics of energy

reserves (E) are based upon a well established template (Clark and Mangel 2000): E increases by g_i when the forager consumes an item of prey type i , up to a maximum of E_M , and decreases due to metabolic expenditures, as a linear function of time (I assume a constant rate of metabolism, m , for all activity). If E declines to some critical level (0 in this model) the forager dies. The state dynamics of foraging skills are less conventional and require more explanation. The skill level for each prey type i (S_i) can vary between 1 and some maximum, S_M . S_i is incremented by l_i after each capture and handling of prey type i (“learning”) and decremented by f_i after each capture and handling of prey type j , where $j \neq i$. S_i remains unchanged if no prey is encountered. Parameter f_i represents the effect of forgetting, or “interference”; that is, the limited capacity of animals to master or retain complex handling skills for dissimilar prey types (Heinrich et al. 1977, Goulson et al. 1997). I evaluate the effect of varying both l_i and f_i .

Previous studies have shown that acquired experience with a single prey type can affect many aspects of forager physiology and behavior (e.g. Werner et al. 1981, Cunningham and Hughes 1984, Partridge and Green 1985, Croy and Hughes 1991, Laverty 1994, Kandori and Ohsaki 1998, Reiriz et al. 1998, Keasar et al. 2002); here I consider only the effect of S_i on handling efficiency. Realized handling time, h_i , is modeled as a decreasing function of S_i :

$$h_i(S_i) = H_i \left(1 - \left(\frac{\rho(S_i - 1)^\gamma}{(S_M - 1)^\gamma} \right) \right) \quad 33$$

where $0 \leq \rho < 1$ and $0 < \gamma < \infty$. This function exhibits behavior that is intuitively appealing and allows me to explore a variety of biologically plausible scenarios. The first parameter, ρ , determines the magnitude of the learning effect. When $\rho = 0$, h_i is fixed at H_i , resulting in

no realized effect of acquired experience. As ρ approaches 1, learning has an increasingly strong effect on handling time, with h_i reaching its minimum value when $s_i = S_M$. The second parameter, γ , determines the temporal dynamics of the learning process. When $\gamma = 1$, h_i decreases linearly with S_i (this will be referred to hereafter as a linear learning curve). When $\gamma < 1$, h_i decreases rapidly with initial increments of S_i , but the rate of change decelerates and becomes asymptotic as S_i approaches S_M (this will be referred to hereafter as an “r-shaped” learning curve). When $\gamma > 1$, h_i decreases slowly with initial increments of S_i , but the rate of change accelerates as S_i approaches S_M (this will be referred to hereafter as a “J-shaped” learning curve).

For both the SDPM and the IBM models I consider a simple system in which foragers have two potential prey types to choose from: prey type 1, characterized by high energy content and long handling time, and prey type 2, characterized by lower energy content and shorter handling time (Table 3.1). With handling times set to their baseline values, the net energy return from prey type 1 (g_1/H_1) is higher than that from prey type 2 (g_2/H_2), making it the default “preferred” prey in the absence of any learning effect. It is worth emphasizing that the effect of learning is fundamental to all results presented here: if $\rho = 0$ then my theoretical framework collapses to the simple optimal prey selection model (Schoener 1971, Pulliam 1974, Charnov 1976, Stephens and Krebs 1986). Specifically, if λ_1 is the encounter rate for prey type 1, then a forager is predicted to ignore prey type 2 if:

$$\lambda_1 > \frac{g_2}{g_1} \left(\frac{1}{H_2 - H_1} \right) \quad 34$$

otherwise the forager is expected to generalize (capture either prey type when encountered).

Stochastic Dynamic Programming Model

The key feature of a SDPM is that each potential decision available to an individual at any time t can be evaluated in terms of its expected fitness consequences at time $t+1$, and thus the expected behavior depends on both the past experience, the current state and the probable future state of the forager (Mangel and Clark 1988, Clark and Mangel 2000). I equate fitness with reproductive success at time T , where reproductive success may be defined as the number and/or viability of offspring produced. The fitness of an individual at time t , $F(e, s_1, s_2, t)$, is the maximum expected reproductive success at T , given $E(t) = e$, $S_1(t) = s_1$, and $S_2(t) = s_2$. At time T , fitness is an increasing function of the individual's remaining energy reserves:

$$F(e, s_1, s_2, T) = \frac{\exp\left(\frac{e-\theta}{\phi}\right)}{1 + \exp\left(\frac{e-\theta}{\phi}\right)} \quad 35$$

where θ and ϕ are parameters that together characterize the shape of the relationship between energy reserves and reproductive success (a *logit* function is used so that fitness varies between 0 and 1). This relationship could conceivably take a variety of forms: in sea otters, for instance, the probability of successfully rearing offspring is an s-shaped (logistic) function of the mother's energy reserves (Monson et al. 2000). I evaluate a range of potential values for θ and ϕ (Table 3.1), allowing for s-shaped, r-shaped, j-shaped or linear relationships.

For times previous to T , fitness is calculated using the dynamic programming equation:

$$\begin{aligned}
F(e, s_1, s_2, t) = & \left[\lambda_1 \max \{ F(e - m, s_1, s_2, t + 1), F(e + g_1 - m(1 + h_1(S_1)), s_1 + l_1, s_2 - f_2, t + 1 + h_1(S_1)) \} \right. \\
& + \lambda_2 \max \{ F(e - m, s_1, s_2, t + 1), F(e + g_2 - m(1 + h_2(S_2)), s_1 - f_1, s_2 + l_2, t + 1 + h_2(S_2)) \} \\
& \left. + (1 - \sum_i \lambda_i) F(e - m, s_1, s_2, t + 1) \right] \exp(-M)
\end{aligned} \tag{36}$$

with the understanding that appropriate constraints apply to each state variable, as described above, and that realized handling times h_1 and h_2 are functions of S_1 and S_2 (respectively) as described by equation 33. The last term accounts for the probability of incidental mortality (M), defined as death due to causes other than depletion of energy reserves. The solution to the dynamic programming equation (or DPE) is calculated iteratively, moving backwards in time from $t = T-1$ to $t = 1$. Solving the DPE provides both the expected fitness and the predicted behavior of a forager – to capture or ignore prey of type 1 or 2, when encountered – at each time, t , as a function of the current values of its state variables. The predicted behavior is determined by evaluating the first two rows of equation 36 (row 1 corresponds to prey 1 and row 2 corresponds to prey 2). I solve the DPE over a wide range of values for all parameters, to assess the effect of each parameter on the decision matrix, the multidimensional array of predicted “best decisions” at all possible values of E , S_1 , S_2 , and t (Mangel and Clark 1988, Clark and Mangel 2000). Table 3.1 gives the baseline values of each parameter used for the SDPM, as well as the range of values evaluated.

Individually Based Model

I next design an IBM to conduct replicated simulations of forager populations. This allows me to explore population-level dynamics of foraging specializations in a simple world with two prey types, where the behavior of each individual at any given time is determined by the current environmental conditions (i.e. prey population densities) and the individual’s own state. One possible way of specifying the appropriate decision rules for

individuals in the IBM would be to use results from the SDPM to specify optimal behavior under every possible set of conditions. However, the results of the SDPM (Table 3.2; Figure 3.1) suggested that a much simpler function could be used to closely approximate the predictions of the decision matrices, thereby providing a simple set of “rules of thumb”. Specifically, a forager that has encountered an item of prey type i will either capture or keep searching based primarily on the state of its skill level for the encountered prey (S_i), its skill level for alternative prey types included in its diet ($S_j, j \neq i$), and the current encounter rates for all prey types ($\lambda_1, \lambda_2 \dots \lambda_n$). I use a 4-parameter function to define an appropriate decision cut-off value for each prey type: if the skill level for prey type i is below the cut-off value then the individual will reject it, otherwise it will accept it. Specifically, in the case of 2 possible prey types, an individual is predicted to reject prey type 2 (and thus specialize on prey type 1) if:

$$S_2 < \alpha_1(S_1 - \omega_1 S_1^2 + \varepsilon_1) + \delta_1 \left(\frac{\lambda_1}{\lambda_2} \sum_{i=1:n} \lambda_i \right) \quad 37$$

Similarly, it is predicted to reject prey type 1 (and thus specialize on type 2) if:

$$S_1 < \alpha_2(S_2 - \omega_2 S_2^2 + \varepsilon_2) + \delta_2 \left(\frac{\lambda_2}{\lambda_1} \sum_{i=1:n} \lambda_i \right) \quad 38$$

The parameter α_j determines the magnitude of the effect of a forager’s skill level for alternative prey type j , ω_j allows for non-linearity of the function with respect to skill, ε_j is a constant and δ_j determines the effect of prey abundance (i.e. the encounter rate of prey j relative to prey i , scaled to the encounter rate for all prey types). Depending on the values of α , ω , ε , and δ , equations 37 and 38 can result in rules of thumb corresponding to a wide array of alternative strategies: always specialize on one prey type irrespective of prey encounter rates, always generalize, specialize on one prey type if that prey is very abundant,

or anything in between. How then to select appropriate parameter values? An important feature of the IBM approach is that the dynamics of interest arise as emergent properties from the cumulative behavior of many individuals, each following very simple decision rules (Railsback 2001); moreover, the decision-rules themselves are among the emergent properties. Accordingly, I use natural selection simulations to parameterize the decision rule function for each hypothetical scenario, as I explore the effect of model variables.

The basic algorithm for the IBM is: initialize the population (with starting values for each state variable selected randomly) and, starting at time $t = 0$, allow all individuals to actively forage for T time units (T can be thought of as one year in the life of the forager). The sequence of prey encounters for each individual is entirely stochastic, and individuals accept or reject encountered prey items following the rules of thumb described above. State variable dynamics are identical to those described for the SDPM. Any individuals whose energy reserves dip to 0 are assumed to die; additionally, incidental sources of mortality (e.g. disease, predation) can strike any individual at any time during the year with probability M . At the end of each year, those individuals that are still alive can reproduce: for simplicity, I assume an all-female population. Some proportion of the parent's energy reserves (arbitrarily set to $\frac{1}{4}$) are transferred to the offspring, which survive to weaning with probability W , where W is given by equation 35 (offspring viability is thus a function of the parent's energy reserves at year-end). After the year-end reproduction period, all adults and surviving new recruits begin another year of foraging.

I make a number of modifications to the basic IBM algorithm to produce a life history pattern typical of the larger vertebrates for which both alternative foraging specializations and cultural transmission have been reported (e.g. sea otters, cetaceans,

primates). The age of first reproduction is delayed until 2 years of age, and annual reproductive output consists of a single offspring. Incidental mortality of adults (M) is low until the age of senescence (5 years), after which M increases greatly, thereby limiting maximum lifespan to approximately 10 years. Together, these life history traits result in a relatively low intrinsic growth rate for the population ($r_{max} \cong 0.15$). To prevent forager populations from growing exponentially and indefinitely, I add density dependence such that M increases with population size, resulting in a carrying capacity for the forager population of approximately 1000 individuals.

The mean encounter rate for each prey type, λ_i , is re-calculated at the beginning of each year:

$$\lambda_{i,y} = \frac{N_{i,y}}{\sum_i K_i} \quad 39$$

where $N_{i,y}$ is the population size of prey species i at year y , and K_i is the carrying capacity of the i^{th} prey species. By re-calculating encounter rates only once per year, I assume that intra-annual variation in prey population size is insignificant relative to inter-annual variation.

Given the large size of prey populations relative to the forager population, I believe this is a reasonable assumption. I further assume that prey population recruitment is discrete, annual, and occurs at year-end:

$$N_{i,y+1} = (N_{i,y} - C_i) + r_i (N_{i,y} - C_i) \left(1 - \frac{(N_{i,y} - C_i)}{K_i} \right) \quad 40$$

where C_i is the number of individuals of prey population i consumed by predators during year y . Per-capita mortality from predation is typically incorporated into r , the intrinsic rate of population increase; equation 40 tracks the net effect of predation as a separate term, thus

facilitating the consideration of two alternative scenarios of predator-prey interaction. Under the first scenario, the predator population has the potential to limit its own prey populations, so that the number of prey individuals consumed by the predator population impacts the prey population size the following year. This scenario allows for frequency dependent benefits of a particular prey specialization, and will be referred to hereafter simply as frequency dependence. Under the second scenario, the predator does not limit its own prey populations and C is held constant, so that the dynamics of the prey population are effectively decoupled from predation by the focal population of foragers. In this scenario C represents loss of prey individuals to all sources of mortality, and predation by the focal population of foragers is assumed to be entirely compensatory. Scenarios one and two represent two extreme cases: intermediate levels of frequency dependence can also be modeled by varying p , the proportion of C that is constant. I define the intensity of frequency dependence as $1-p$: this index provides a measure of the relative impact of predation by the forager on prey population dynamics.

In scenarios with or without frequency dependence, r accounts for net recruitment of new individuals into the prey population, and is assumed to be subject to environmental stochasticity. To model stochasticity, a mean value for r is specified (arbitrarily) for each simulation, and annual deviations from the mean are modeled as correlated random deviates with mean of 0, coefficient of variation ψ and first-order temporal autocorrelation of κ (following methods of Doak and Morris 2002). By adjusting the parameters ψ and κ I can vary the magnitude and frequency of fluctuations in prey abundance, and thus evaluate how patterns of variation in prey populations affect the temporal dynamics of foraging specializations.

I evaluate the temporal dynamics of foraging behavior both with and without the cultural transmission of foraging skills. I consider only matrilineal (vertical) transmission, whereby a parent transfers some of its acquired skills to its offspring. Specifically, the skill of a new forager recruited to the adult population is:

$$S_{k,i} = \beta(Y_{k,i}) + \chi_{\mu,\sigma} \quad 41$$

where $S_{k,i}$ is the initial skill level of forager k for prey type i , $Y_{k,i}$ is the skill level of k 's mother for prey type i , β is the fraction of $Y_{k,i}$ inherited by the offspring and thus represents the effect of cultural transmission, and $\chi_{\mu,\sigma}$ is a normal random deviate with mean μ and variance σ^2 , representing the effect of random variation in innate foraging skills. I assess the effect of phenotypic variation by comparing low vs. high variation in innate foraging skills. I evaluate the effect of cultural transmission on the temporal dynamics of foraging specialization by varying β from 0 (no cultural transmission) to 0.9 (very strong cultural transmission).

Table 3.1 summarizes the baseline values for all parameters in the IBM, as well as the range of values evaluated. For each unique combination of IBM parameter values, I initialize a starting population with randomly assigned values for the decision rule parameters and treat each unique set of values as a “genotype”. I assume that foraging rules of thumb are heritable and exhibit additive genetic variation (e.g. Kolliker et al. 2000), and I simulate this variation by adding small, random deviations to the decision rule parameters inherited from parents by offspring (deviations are normally distributed with mean = 0). Genotypes can thus drift over generational time, with selection sorting out those combinations of values that produce non-viable strategies (e.g. specializing when generalizing would actually be more profitable, or vice versa). I allow a sufficiently long

period of time (at least 2500 years per replication) for the surviving genotypes to converge to a stable distribution, and I conduct 10 replications of the selection process to ensure that results are repeatable and consistent. A random sub-set of optimal genotypes is then selected from the final distribution, and used for all further simulations.

For each combination, having arrived at appropriate distributions for decision rule parameter values using natural selection simulations, I run 100 replications of 100 years, to evaluate the temporal dynamics of foraging behavior in the population. I quantify the tendency of individuals to be foraging specialists by tracking I , the annual index of specialization. I calculate I as the population average of I_k , the diet overlap between individual forager k and the population:

$$I_k = \sum_i \min \left(\frac{n_{i,k}}{\sum_i n_{i,k}}, \frac{\sum_k n_{i,k}}{\sum_k \sum_i n_{i,k}} \right) \quad 42$$

where $n_{i,k}$ is the number of items of prey type i consumed by individual forager k during the year (Bolnick et al. 2002). For individuals that specialize on a single prey type, I_k takes on the value q_i , where q_i is the proportion of the population's diet composed of the i^{th} prey type. In contrast, I_k is equal to 1 for generalists that consume resources in direct proportion to the population as a whole. Small values of I thus reflect a high prevalence of specialization in the population. In addition to tracking I , the frequency of co-occurrence of alternative specialists in each simulation is also measured: I define this index as the proportion of years in which prey type-1 specialists and prey type-2 specialists each make up at least 10% of the forager population (I reason that co-occurrence implies that specialists of each type are sufficiently abundant to be both observable and biologically relevant, and individuals are considered to be specialists if their diet consists solely of one prey type). Finally, I track the

between-year variation in the frequency of specialists of each type (measured as the CV, or coefficient of variance).

In total I evaluate 100 unique combinations of IBM parameter values. I determine the sensitivity of the IBM results to 8 model parameters (ρ , l_i , f_i , γ , β , ψ , κ , and the intensity of frequency dependence) using multiple regression analysis: specifically, I calculate the portion of variance in two response variables (the index of specialization, I , and the frequency of co-occurrence of alternative specialists) explained by each parameter, after accounting for variance due to all other parameters. Individual variance components are estimated by their partial coefficients of determination ($r^2_{y1.2\dots n}$), following Neter (1990). To account for uncertainty, I calculate the 95% confidence intervals for the $r^2_{y1.2\dots n}$ estimates using the bootstrap- t method (DiCiccio and Efron 1996).

Unless otherwise indicated, effects associated with variation in each parameter are reported assuming that all other parameters are held at their baseline values (Table 3.1). Error bars in figures and all ranges of values reported in the text (in parentheses) represent the 95% confidence intervals of the statistic in question.

Results

Stochastic Dynamic Programming Model

The results of the SDPM suggest that when skill level has a sufficiently large effect on prey handling times (e.g. $\rho \geq 0.5$), and when learning of prey-specific handling skills is slow enough relative to the organism's life span, there will be certain conditions under which a forager will specialize on one prey type or the other, and other conditions under which it will generalize. More specifically, the expected behavior of a forager can be expressed as a function of its relative skill levels for each prey type (Figure 3.1).

Varying the values of θ and ϕ has no appreciable effect on the model predictions, causing only slight differences in expected behavior as t approaches T and as S_1 or S_2 approach S_M . Consequently, for all further analyses I hold θ and ϕ fixed at values that result in a s-shaped fitness function: I chose these particular values because they approximate the functional relationship between energy reserves and reproductive success described for sea otters (Monson et al. 2000). Varying other model parameters (within the ranges indicated in Table 3.1) has the effect of changing the relative size of each of the 3 regions of the decision matrix (Figure 3.1; Table 3.2).

Population Dynamics

The frequency of specialists vs. generalists at the population level, as predicted by the IBM, is generally consistent with the individual responses predicted by the SDPM. In particular, the prevalence of specialists in the population at any given time varies with the basic model parameters in the direction predicted by the results of Table 2 (Figure 3.2).

The degree of innate variation in the foraging skills of new recruits has a strong effect on both the prevalence of specialists and the frequency of co-occurring alternative specializations: when all other parameters are held constant (and assuming no frequency dependence or cultural transmission), increasing σ^2 from the minimum to the maximum allowed value (Table 3.1) causes a decrease in I (from 0.75 ± 0.014 to 0.69 ± 0.012) and an increase in the frequency with which co-occurring alternative specialists are observed (from 0.35 ± 0.091 to 0.65 ± 0.082). However, other factors that affect the temporal dynamics of specialization in the population – specifically, frequency dependent effects, cultural transmission, and stochastic variation in prey species abundance – have the same qualitative effects irrespective of the magnitude of innate variation in foraging skills, therefore I report all successive results for a single, intermediate level of variance ($\sigma^2 = S_M/10$).

The temporal dynamics of foraging specializations differ significantly between simulations with purely stochastic vs. frequency dependent prey dynamics: frequency dependence results in a far higher probability of observing alternative specializations (Figure 3.3). This difference appears to be largely the result of a decrease in the temporal variability of specializations, rather than an increase in the overall prevalence of specialists: assuming baseline values for all parameters, the between-year variability in the frequency of type 1 specialists is greater for simulations without frequency dependence ($CV = 0.54 \pm 0.13$) than for simulations with frequency dependence ($CV = 0.35 \pm 0.02$), and the pattern is identical for type 2 specialists ($CV = 0.81 \pm 0.26$ for simulations without frequency dependence vs. 0.44 ± 0.02 for simulations with frequency dependence).

The ability of individual foragers to pass on learned skills to offspring via cultural transmission ($\beta > 0$) has a striking effect on the temporal dynamics of foraging

specializations. Under certain conditions, a 30% increase in the relative strength of cultural transmission (from $\beta = 0.5$ to $\beta = 0.8$) results in a 100% increase in the frequency of co-occurring alternative specializations (Figure 3.3). The existence of frequency dependent effects has a positive interaction with the effect of cultural transmission (Figure 3.3A), and there are also interactions between β and other parameters such as the rate of forgetting (f_i) and the shape of the learning curve (γ). In simulations with an r-shaped learning curve, the introduction of cultural transmission results in a greater relative increase in the frequency of co-occurring alternative specializations than simulations with a linear or J-shaped learning curve (Figure 3.3B). Differences in the temporal dynamics of foraging specializations in simulations with and without cultural transmission can be explained in part by the selective effects of cultural transmission on the decision rules themselves (Figure 3.4).

The degree of stochastic temporal variation in prey population abundance has some effect on the frequency of co-occurring alternative specializations, although less striking than the effects of frequency dependence or cultural transmission. An increase in the magnitude of stochastic variation (ψ) is associated with a decrease in the frequency of co-occurring alternative specialists (0.48 ± 0.08 when $\psi = 0.25$ vs. 0.27 ± 0.07 when $\psi = 2.0$). The relative speed of stochastic changes in prey populations also affects the frequency of co-occurrence, although this effect is only statistically significant in simulations with cultural transmission: increased temporal autocorrelation of prey abundance is associated with a lower frequency of co-occurring alternative specialists (0.57 ± 0.07 when $\kappa = 0.2$ vs. 0.48 ± 0.07 when $\kappa = 0.7$, and $\beta = 0.8$ in both cases). Low values of κ (resulting in rapid changes in prey abundance) are associated with greater co-occurrence of alternative specializations and

less temporal variability in the frequency of specialists (CV of 0.42 ± 0.04 when $\kappa = 0.2$ vs. CV of 0.52 ± 0.04 when $\kappa = 0.7$, as measured for type 1 specialists).

The model parameters with the greatest relative effects on the IBM results are (in decreasing order of their associated sensitivities) the intensity of the learning effect (ρ), the intensity of frequency dependence, and the rate of forgetting (f_i) (Figure 3.5). The model results are less sensitive to the degree of cultural transmission (β), the rate of learning (l_i), the shape of the learning curve (γ), and the degree of stochasticity of prey populations (ψ and κ), at least within the ranges of values explored here.

Discussion

The results of the SDPM and the IBM confirm the primary prediction of Hughes' (1979) model: the ability of animals to learn and improve foraging skills through experience leads to an increased tendency to specialize, and can also result in individual switching from one prey specialization to another. Given the results of both models, I predict that the following behavioral, physiological and/or life history characteristics will be associated with increased levels of specialization: 1) increased experience with one particular prey type has a strong effect on some component of foraging (e.g. handling time, capture success, digestion efficiency); 2) the rate at which new skills are acquired through experience is relatively slow; 3) there is limited ability to learn or retain complex learned skills for one prey type when many other prey types are included in the diet (skills are either forgotten through lack of use, or lost via interference with new skills); 4) the learning curve for new foraging skills is J-shaped, rather than linear or r-shaped; 5) the forager does not carry extensive energy reserves, or at least it cannot rely on such stores to supplement poor foraging performance over the time required to learn new skills; 6) metabolic costs of foraging are high relative to energy reserves, or to the energy gained by each prey capture; 7) the forager is able to transfer learned skills to offspring, either actively (via teaching), passively (no direct teaching, but the offspring nonetheless learns skills through observation or mimicking of the parent, e.g. Stoinski et al. 2001) or through stimulus enhancement (e.g. Visalberghi and Addessi 2001). In addition to these characteristics of the forager, the following prey species characteristics are also predicted to result in an increased degree of specialization and/or likelihood of alternative specialists: 8) the encounter rate for all prey types is relatively high; 9) the population growth rates or abundance of the prey species are significantly impacted by

predation pressure by the forager, resulting in frequency/density dependent benefits of alternative specialist strategies (Partridge and Green 1985, Estes et al. 2003); 10) stochastic variation in the abundance of the prey species (i.e. variation not due to predation by the forager) is neither too extreme in magnitude nor too “slow” with respect to the time required for an individual forager to learn new foraging skills.

Some of these predictions – particularly predictions 1 and 2 – are immediate consequences of the fundamental assumptions of the model. Clearly if there is little impact of learned skills on any of the components of foraging success, or if new skills can be acquired so quickly that there is little cost to doing so, then some (or all) of the potential benefits of specialization are negated. Some of the other predictions, however, are less intuitive, and bear closer examination. Prediction 3, that specialization is more likely when specific skills for one prey type are forgotten or lost when the forager switches to different prey, is essentially Darwin’s interference hypothesis (Darwin 1876, Heinrich et al. 1977, Goulson et al. 1997). Interference in handling skills for different prey types, resulting in reduced handling efficiency of generalists vs. specialists, has been shown for diverse taxa (e.g. Cunningham and Hughes 1984, Lavery and Plowright 1988, Goulson et al. 1997, Gegear and Lavery 1998) and may be a common characteristic among predators with multiple, dissimilar prey types. In the current model, the interference effect was introduced using parameter f_i , however the precise nature and strength of an interference effect is likely to vary widely from system to system, and may be countered to some degree by the ability to transfer learned skills from one prey type to novel prey types (Hughes and O'Brien 2001). The results of the IBM were highly sensitive to this parameter (Figure 3.5), suggesting that

experimental quantification of the interference effect may provide a fruitful area for further research.

The results of both the SDPM and the IBM suggest that a J-shaped learning curve is more likely to result in specialization than an r-shaped curve, although the shape of the learning curve has a greater effect on the likelihood of co-occurring specializations than it does on the prevalence of specialization itself (Figure 3.5). A J-shaped learning curve means that an individual's initial experiences with a novel prey type will have very little effect on its handling efficiency, and thus the relative cost of switching to a new prey type is greater than for an r-shaped curve. In those few cases where the learning dynamics for novel prey types have been accurately measured, the result has usually been an r-shaped learning curve (Cunningham and Hughes 1984, Croy and Hughes 1991, Hughes and O'Brien 2001). However, the shape and slope of the learning curve will likely differ greatly between different prey types, even within the diet of a single predator species (Laverty 1980, Laverty 1994). A slower, J-shaped learning curve may be more typical for apex predators such as sea otters (Estes et al. 2003), which have a wide potential prey base that includes dissimilar taxa at multiple trophic levels, some requiring complex handling skills. At the extreme, foragers that utilize highly complex foraging techniques or use tools to manipulate prey may require years to become highly adept at a particular prey handling technique (Huffman and Quiatt 1986, Guinet and Bouvier 1995, Estes et al. 2003). In tool-using foragers the learning curve may be an exaggerated J-shape, or even a step function, with a long "experimental period" resulting in virtually no increase in skill followed by a fairly rapid improvement period as the tool is mastered (Huffman and Quiatt 1986). A prolonged period of offspring dependency would be particularly adaptive in the case of strongly J-shaped learning curves,

because the offspring can get past the initial slow-learning period and perfect its skills while still “subsidized” by the parent.

A prolonged period of offspring dependency also allows for the possibility of transmission of skills from parent to offspring via cultural transmission. My model suggests that cultural transmission can have a strong effect on the degree of specialization and the likelihood of observing alternative specializations within one population (Figure 3.5).

Cultural transmission, as I have modeled it, ensures that new recruits tend to start out their independent life with honed skills for one prey type but minimal skills for alternative prey, rather than intermediate skills for all prey. Such a tendency will result in an increased degree of specialization within the population; however, this only accounts for part of the observed effect. When I use identical decision rules for simulations run with and without cultural transmission, the difference in the degree of specialization is less pronounced than when I use appropriate decision rules for each simulation (and this is the case irrespective of the value of other model parameters; Figure 3.4), because selection results in different optimal decision rules in populations exhibiting cultural transmission. The difference may arise in part because, in populations exhibiting cultural transmission, the inclusive fitness of individuals is not just a function of energy reserves transferred to offspring, but also a function of the skills that can be transferred. Under certain conditions this will lead to a selective trade-off between competing rules of thumb: although generalizing would be more likely to result in higher energy reserves at reproduction, continued specialization would be more likely to result in effective foraging skills to transfer to future offspring.

Cultural transmission represents one solution to the problem posed by prey types whose relative profitability depends on complex, hard to master foraging skills. An

alternative solution to the same problem is a “hard-wired” solution, i.e. genetically controlled behavioral, morphological or physiological adaptation to the specific requirements of a particular prey type. In the latter case, individual foragers are expected to specialize on the prey type appropriate to their particular “hard-wired” phenotype (Werner et al. 1981, Ehlinger 1990). This hard-wired solution (or trophic polymorphism, sensu Robinson and Wilson 1994, Smith and Skúlason 1996), has been documented for many taxa (e.g. Smith 1990, Robinson and Wilson 1995, Gianni Christopher et al. 1996). In systems where the suite of potential prey is not sufficiently stable over time, however, trophic polymorphism may be less adaptive than a combination of behavioral flexibility, learning ability and cultural transmission, the latter allowing populations to rapidly adjust to changes in prey abundance, adopt new prey species, or otherwise accommodate changing foraging requirements (Bonner 1980).

In addition to increasing the prevalence of specialization, cultural transmission is associated with an increase in the co-occurrence of alternative specializations, likely due to an intergenerational lag effect created by transmission of skills from mother to offspring. As the relative abundance of different prey populations changes from year to year, the predicted “optimal” behavior for naive new recruits also changes (e.g. from specialization on prey type 1, to generalization, to specialization on prey type 2). In a population with no cultural transmission, the result of such changes is substantial annual variation in the prevalence of specialists, and the population will often be devoid of specialists of a given type. On the other hand, if new recruits inherit prey-specific skills from their parents, it may remain profitable for them to specialize on one prey type even when its encounter rate decreases substantially. Matrilineal transmission of skills can thus delay the time it takes for one

specialization to disappear from the population altogether, thereby increasing the likelihood of observing alternative specializations within the population at any given time. If there is also frequency/density dependent limitation of prey populations by the forager population, such that the abundance of each prey type tends to cycle from low to high (but always out of step with other prey types), then the intergenerational lag created by cultural transmission may act to prevent specializations from ever disappearing entirely from the population. The positive interaction between frequency dependence and cultural transmission (Figure 3.3a) supports such a scenario.

The degree to which dynamics of the prey populations were controlled by predation pressure from the forager population strongly impacted simulation results (Figure 3.5). Frequency dependence tends to result in regular, out-of-step oscillations in the relative abundance of alternative prey populations, and at the same time it tends to limit the absolute magnitude of such variation. Similarly, in the absence of frequency dependence, the nature of stochastic variation in prey population abundance determined the degree of co-occurrence of alternative specializations. In populations where the year-to-year changes in prey population abundance are low (corresponding to high temporal autocorrelation), individual learning is able to “keep up” with variation in encounter rates, and thus the relative frequency of specialists essentially tracks prey variation. Conversely, in populations where the year-to-year changes in prey population abundance are high (corresponding to frequency dependence, or low temporal autocorrelation), individual learning cannot keep up with variation and there is a lag, similar to that created by cultural transmission, which dampens variation in the abundance of specialists and increases the likelihood of observing alternative specializations within the population at any given time. However, if variation in prey

abundance is too great in magnitude then any type of specialization can become risky – a prey type that is very profitable one year may be extremely rare the next – and so a “risk-spreading” strategy of generalization becomes more prevalent.

The general patterns predicted by the models should be broadly applicable to many animal species. Nonetheless, I must highlight a number of qualifications. The most important caveat concerns the quantitative results reported, which (in contrast to the qualitative patterns highlighted above) depend entirely on the specific parameter values chosen (arbitrarily) for the simulations. For example, the co-occurrence of specialists for both prey types in the absence of frequency dependence or cultural transmission depended upon a) the range of prey-specific parameters being set so that either prey type could be “preferred prey” under at least some realized combinations of prey abundance and skill levels; and b) the existence of some variation in the initial skill levels of new recruits, corresponding to continuous phenotypic variation (Verbeek et al. 1994). In the interest of generality, the underlying structure of the models also reflected some overly simplistic assumptions: for example, I assumed that energy was the sole limiting factor for my hypothetical forager, and that there were no other relevant constraints or decision criteria (e.g. no specific nutritional requirements, no elevated predation risks associated with one prey type, etc.). Incorporating more than 2 prey types, and including multiple constraints and decision criteria, would undoubtedly result in more complex dynamics. Future elaborations of this approach should also include some evaluation of the effect of sensory and memory limitation of individuals, and thus the potential for errors in individual assessments of relative prey abundance (Hirvonen et al. 1999).

Despite the caveats mentioned above, I believe that the general patterns observed allow me to suggest some explicit tests that could be used to either falsify or lend support to the model results (Table 3). The first 4 suggestions in Table 3 describe controlled experiments that could be performed in the laboratory or in highly tractable study systems conducive to manipulative field experiments (e.g. insect foragers: Gegeer and Lavery 1998). Many fish species, such as bluegill sunfish (*Lepomis macrochirus*), would provide excellent study systems for these types of manipulations because it is possible to manipulate foraging conditions or food resources, and alternative specializations are already known to occur (Werner et al. 1981, Wildhaber and Crowder 1995). Indeed, the first suggested manipulation (decreasing food resources and measuring tendency to specialize) has already been tested to some degree by Werner *et al.* (1981), with results supportive of the patterns predicted here. Suggestions 5–9 in Table 3 describe possible field studies involving inter- or intra-specific comparisons. Comparative studies would necessarily provide weaker tests of the model predictions; however, such studies could nonetheless provide further examples and support (or lack of support) for the model predictions. For example, comparisons of the degree of specialization on prey types having different learning curves (Table 3, #8) could be conducted with species such as bumble bees (*Bombus sp.*), where variable learning rates have already been described (Lavery 1994). Multi-year studies of species such as the Cocos Island finch (*Pinaroloxias inornata*), for which alternative specializations have been reported (Werner and Sherry 1987), would allow testing of the expected relationship between the degree of specialization and the abundance of energy reserves (Table 3, #9). Intra-specific comparisons of populations that utilize different suites of prey in different locations, and/or occur at differing population densities, can be used to test for correlations

between specialization and prey-specific learning curves or inter-annual variance (Table 3, #7): sea otters (*Enhydra lutris*) provide an excellent study system for such comparisons, because different populations in Alaska and California utilize highly diverse prey assemblages (Riedman and Estes 1990) and cover the full spectrum of possible population densities (Estes 1990, Estes et al. 1996).

In the recent foraging theory literature much attention has been focused on the importance of individual learning and memory limitations on foraging behavior (e.g. Dukas 1998, Shettleworth 1998); however, such considerations are rarely (if ever) considered at the level of community ecology, where food web interactions are considered to be characteristic of populations. The conceptual framework developed here suggests that the ability of foragers to learn and transmit skills via cultural transmission can have a significant effect on the degree of specialization within a forager population, and can lead to the co-existence of alternative specializations. I propose that individual variation should be incorporated into community interaction webs: for example, a single population of foragers might be functionally equivalent to several co-existing populations of predators with different suites of trophic interactions. Variation between individuals often represents more than just a statistical nuisance, and needs to be more realistically incorporated into our thinking about animal populations.

Tables

Table 3.1 A summary of model parameters, their baseline values, and the range of values evaluated. Where two sets of values are provided, the first applies to prey type 1 and the second to prey type 2.

Parameter	Definition and/or effect of parameter	Baseline	Range of values
T	Number of time intervals per model run	50	N/A
E_M	Maximum level of individual energy reserves	20	N/A
S_M	Maximum skill level for prey type i	20	N/A
g_i	Energy gained by consuming one item of prey type i	7, 4	N/A
H_i	Baseline handling time for prey type i	5, 3	N/A
h_i	Realized handling time for prey type i	(See text, equation 2)	
m	Metabolic rate	0.975	0.95 \rightarrow 1
λ_i	Average encounter rate for prey type i	0.3, 0.5	0.1 \rightarrow 0.4, 0.1 \rightarrow 0.6
l_i	Rate at which new skills are learned for prey type i	1	0.3 \rightarrow 1.5
f_i	Rate at which skills are forgotten for prey type i	1	0 \rightarrow 3
ρ	Effect of learned skills on handling time	0.6	0.4 \rightarrow 0.8
γ	Shape of learning curve (r-shaped, linear, J-shaped)	1	0.67 \rightarrow 1.5
θ	Slope of fitness function	$E_M/3$	$E_M/10 \rightarrow E_M$
ϕ	Shape of fitness function	$E_M/10$	$E_M/20 \rightarrow E_M/2$
M	Incidental mortality rate	0.001	0.0002 \rightarrow 0.002

Table 3.1 (continued), Additional Parameters for Individually Based Model

Parameter	Definition and/or effect of parameter	Baseline	Range of values
$\alpha_i \omega_i \varepsilon_i \delta_i$	Decision rule function parameters for prey type i	(Unlimited range of values)	
W	Weaning success rate (calculated as a function of parents total energy reserves at reproduction)	(See text, equation 35)	
K_1	Carrying capacity of prey population 1	60000	N/A
K_2	Carrying capacity of prey population 2	80000	N/A
R_1	Mean intrinsic rate of increase of prey population 1	0.15	0.10 \rightarrow 0.30
R_2	Mean intrinsic rate of increase of prey population 2	0.20	0.10 \rightarrow 0.40
ψ	Environmental stochastic variation in r_i (CV)	0.75	0.1 \rightarrow 1.5
κ	First order temporal autocorrelation of r_i	0.5	0.2 \rightarrow 0.7
μ	Mean skill level of new recruits, excluding effect of β	$S_M/3$	N/A
σ^2	Variance in skill level of new recruits	$S_M/10$	$S_M/100 \rightarrow S_M$
β	Effect of cultural transmission, defined as the proportion of parents skills transferred to offspring	0	0 \rightarrow 0.9

Table 3.2. Summary of the effects of the SDPM parameters. The third column refers to the labeled lines in Figure 1 that define the regions of specialization on each prey type.

Change to model parameter	Effect of change on decision matrix	Figure 1
$t \rightarrow T$ (reproduction immanent)	Increased specialization, particularly on prey 1 (high-Energy prey), and reduced region of generalization	1c, 2c
$\uparrow \rho$, effect of skill	Increased region of specialization on both prey types	1c, 2c
$\downarrow \rho$, effect of skill	Decreased region of specialization on 1, and no region of specialization on 2	1b
$\uparrow l_i$, rate of learning new skills	Increased region of generalization	1b, 2b
$\uparrow f_i$, rate of forgetting	Increased region of specialization on both prey types	1c, 2c
$\uparrow \gamma$: learning curve is “J” shaped	Increased region of specialization on both prey types	1c, 2c
$\downarrow \gamma$: learning curve is “r” shaped	Increased region of generalization	1b, 2b
$\downarrow e(t)$, state of energy reserves	Increased region of specialization on both prey types	1c, 2c
$\uparrow E_M$, maximum energy reserves	Increased region of generalization	1b, 2b
$\downarrow E_M$, maximum of energy reserves	Increased region of specialization on both prey types	1c, 2c
$\downarrow m$, metabolic costs	Increased region of generalization	1b, 2b
$\uparrow m$, metabolic costs	Increased region of specialization on both prey types	1c, 2c
$\uparrow \lambda_1, \lambda_2$, encounter rate for all prey	Increased region of specialization on both prey types	1c, 2c
$\downarrow \lambda_1, \lambda_2$, encounter rate for all prey	Increased region of generalization	1b, 2b
$\downarrow \lambda_2$, encounter rate for prey type 2	Increased region of specialization on 1, decreased region of specialization on 2	1c, 2b
$\downarrow \lambda_1$, encounter rate for prey type 1	Increased region of specialization on 2, decreased region of specialization on 1	1b, 2c

Table 3.3 Suggested experiments or comparative studies to test the predictions of the models

Suggested Experiment or Comparison	Predictions
1) Manipulate individual energy reserves (e.g. decrease food abundance)	The degree of specialization will increase as mean abundance of energy reserves decrease
2) Manipulate intensity of frequency dependence (the degree to which predation intensity is coupled to prey population dynamics)	There will be increased co-occurrence of alternative specializations in treatments with frequency dependence
3) Manipulate variation in prey population (increase or decrease the magnitude or frequency of changes in prey abundance)	There will be increased co-occurrence of alternative specializations as prey populations become more temporally variable. There will be decreased co-occurrence of alternative specializations when the rate of change is slow relative to the rate of learning
4) Manipulate metabolic costs of foraging (e.g. increase travel time between patches)	The degree of specialization will increase as metabolic costs increase
5) Compare the frequency of specialization in closely related taxa having different offspring dependency patterns	The degree of specialization will be higher in species having prolonged offspring dependency and known (or suspected) cultural transmission of foraging skills
6) Inter- or intra-specific comparisons of species that do effectively limit their prey populations with other species (or populations) that do not	There will be increased co-occurrence of alternative specializations in species with a greater potential for frequency dependence
7) Intra-specific comparisons of foraging behavior among populations that utilize different suites of prey in different habitats	The degree of specialization will be lower in habitats where there is less individual variation in foraging efficiency (lower value of ρ) or where acquisition of prey-specific foraging skills is rapid (high value of l_i)

Table 3.3 (continued)

Suggested Experiment or Comparison	Predictions
8) Intra-specific comparisons of specialization prevalence associated with particular prey types	<p>The degree of specialization will be highest for those prey types requiring complex manipulation skills (i.e. slowest rate of learning or most J-shaped learning curve)</p> <p>Prey species not requiring complex skills (i.e. rapid rate of learning or r-shaped learning curves) will be ubiquitous in the diet</p>
9) Inter-population comparisons or multi-year studies of foraging behavior incorporating environmental differences or varying population densities	<p>The degree of specialization will be higher in locations or years when population density is high and individuals have fewer energy reserves</p>

Figures

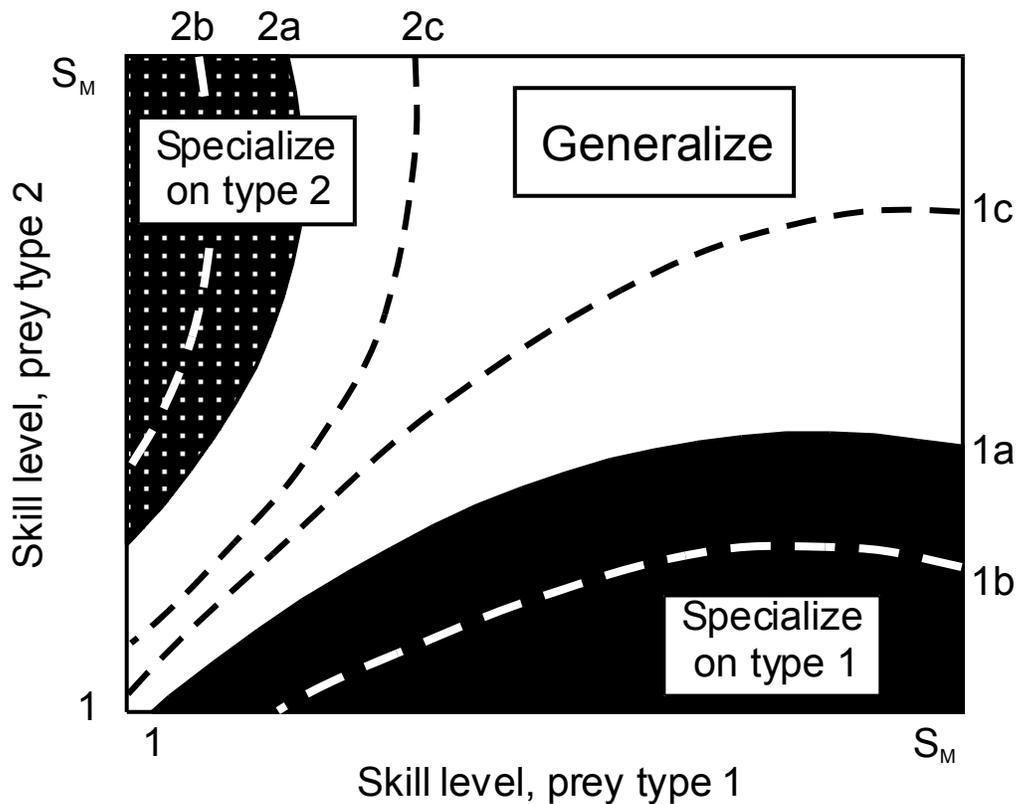


Figure 3.1 Graphical representation of the decision matrix, showing the expected behavior of a forager plotted as a function of its skill level for prey type 1 (horizontal axis) and skill level for prey type 2 (vertical axis) when all parameters are set to their baseline values. The un-shaded area indicates combinations of skill levels where the predicted behavior is to generalize (never reject prey when encountered), the solid-shaded area indicates combinations of skill levels where the predicted behavior is to specialize on prey type 1 (reject prey type 2 when encountered), and the stippled area indicates combinations of skill levels where the predicted behavior is to specialize on prey type 2 (reject prey type 1 when encountered). The dashed lines indicate alternate model outcomes, in which the areas of specialization change as model parameters are varied (see Table 2): lines 1b and 1c show changes in the region of specialization on prey type 1, and lines 2b and 2c show changes in the region of specialization on prey type 2 (1a and 2a correspond to the baseline regions of specialization). The decision rules of thumb used for the Individually Based Model (equations 37 and 38) produce a pattern identical to the one shown here.

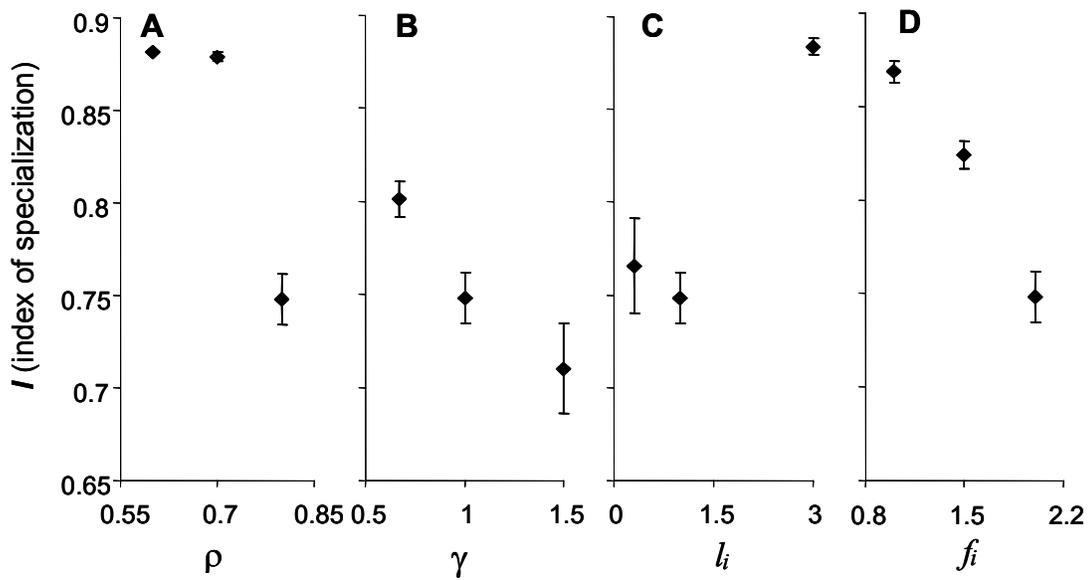


Figure 3.2 The index of specialization (I) as a function of four model parameters: A) the magnitude of the learning effect, ρ (higher values of ρ result in a greater decrease in handling time with experience); B) the shape of the learning curve, γ ($\gamma > 1$ results in a J-shaped learning curve, $\gamma < 1$ results in a r-shaped learning curve); C) the rate at which new skills can be learned, l_i ; and D) the rate at which prey-specific skills are lost by foraging on alternative prey types, f_i . Note that smaller values of I indicate a greater tendency of individuals to specialize rather than generalize, while higher values (approaching 1) occur when individual diets converge on the average diet of population. Error bars represent 95% confidence intervals.

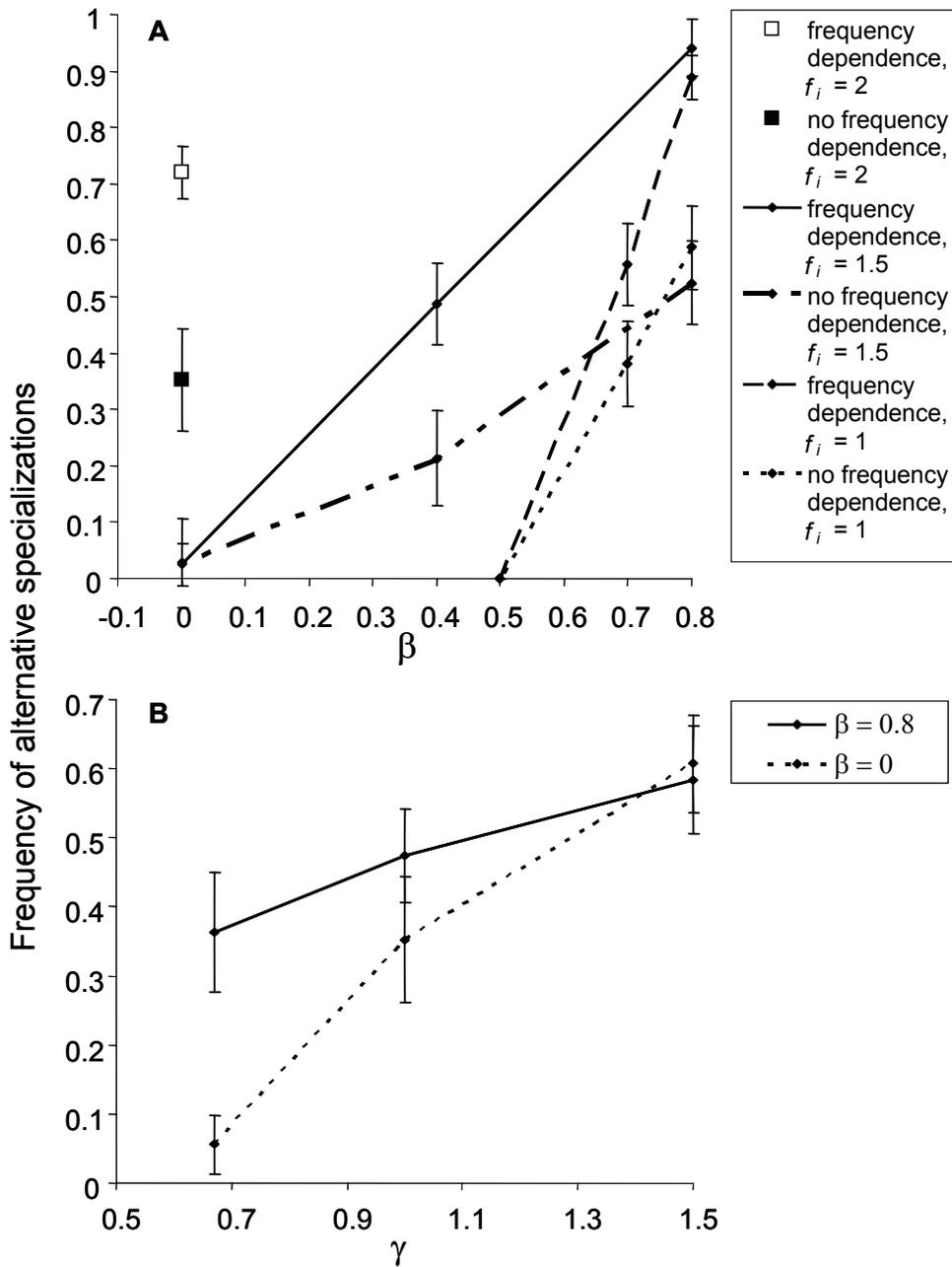


Figure 3.3 The frequency of alternative specializations within a single population plotted as a function of the strength of cultural transmission, β , and the shape of the learning curve, γ . A) Square symbols show the difference between stochastic prey dynamics and frequency dependent prey dynamics when $\beta = 0$ and $f_i = 2$. Diamonds connected by lines summarize the interaction between the effects of frequency dependence, cultural transmission (β) and the rate of forgetting (f_i). B) The effect of varying γ when $\beta = 0$, and when $\beta = 0.8$. Error bars represent 95% confidence intervals.

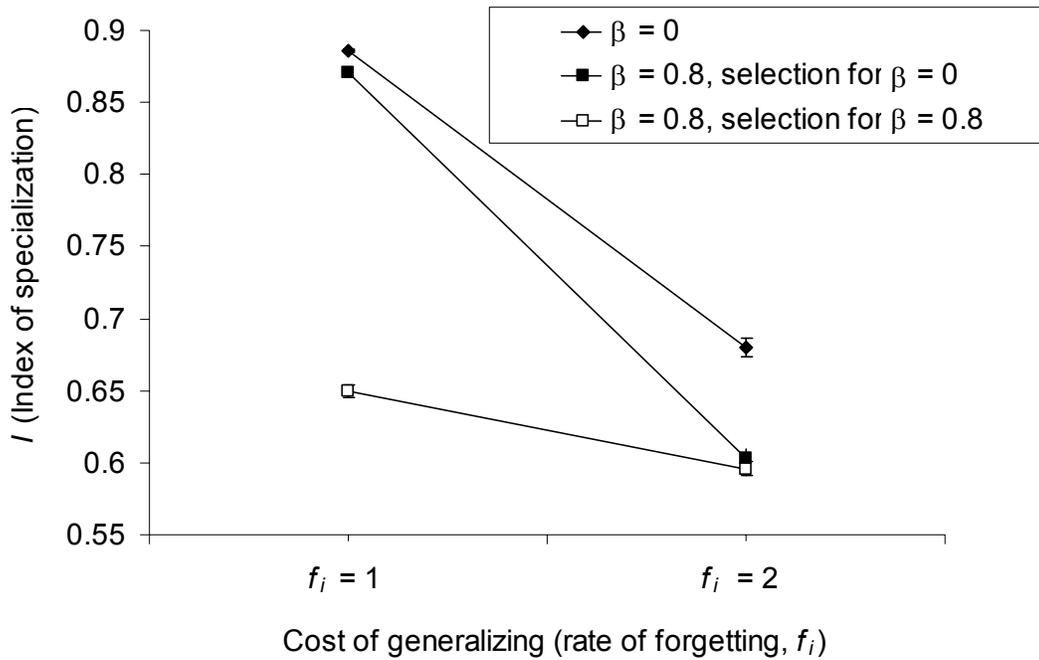


Figure 3.4 The selective effect of cultural transmission on decision rules of thumb when $f_i = 1$ (slow rate of skill loss for generalists) and when $f_i = 2$ (fast rate of skill loss for generalists). Three sets of results are shown: simulations with no cultural transmission ($\beta = 0$), simulations where individual foragers transmitted their foraging skills to offspring ($\beta = 0.8$) but used decision rules selected for under conditions of no cultural transmission ($\beta = 0$), and simulations where individual foragers transmitted their foraging skills to offspring ($\beta = 0.8$) and used appropriately-selected decision rules. Error bars indicate the 95% confidence bound around each point (all points shown are significantly different).

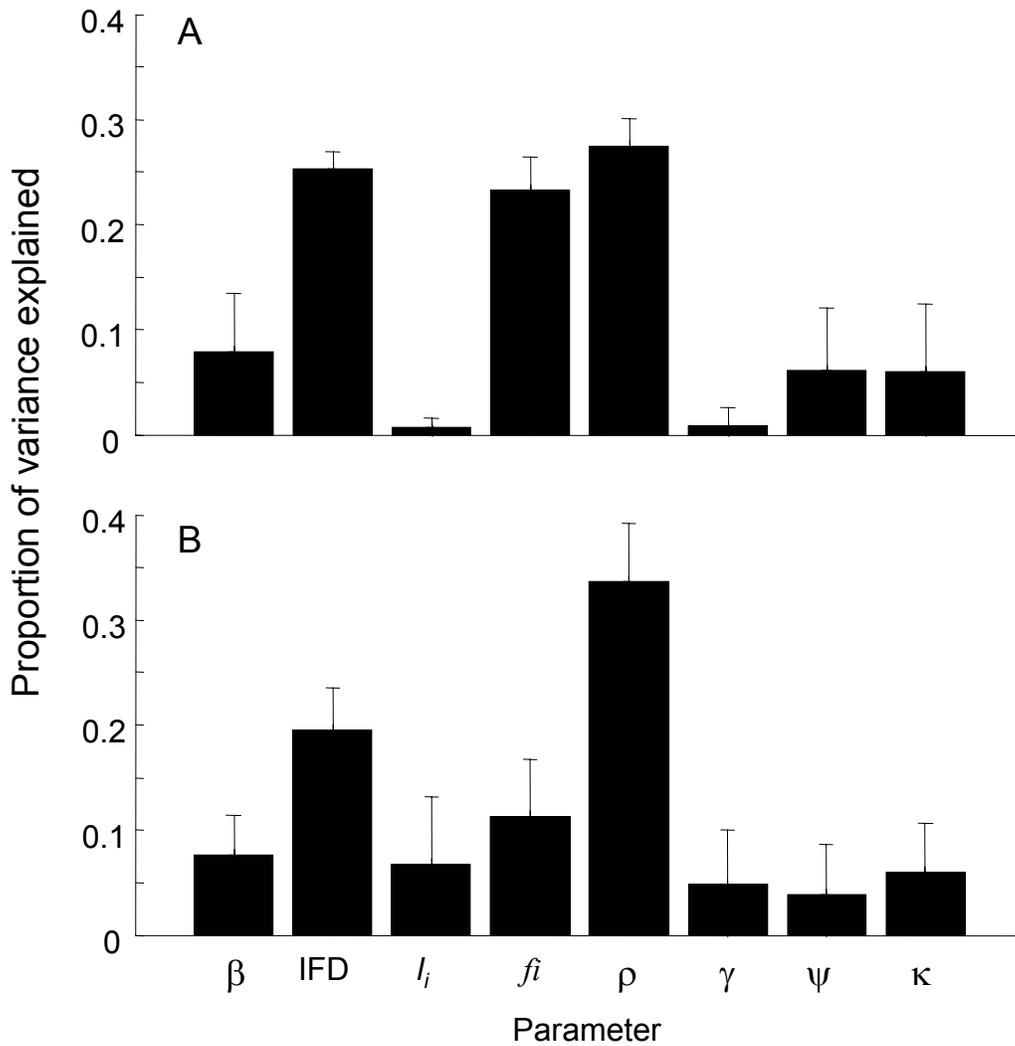


Figure 3.5 The sensitivity of simulation results to 8 of the model parameters: the strength of cultural transmission (β), the intensity of frequency dependence (IFD), the rate at which foraging skills are acquired by learning (l_i), the rate at which foraging skills are lost by forgetting (f_i), the degree to which learning affects handling efficiency (ρ), the shape of the learning curve (γ), the magnitude of stochastic variation in prey population dynamics (ψ) and the degree of temporal autocorrelation in prey population dynamics (κ). A) the relative contribution of each model parameter to variation in I , the index of specialization; B) the relative contribution of each model parameter to variation in the frequency of co-occurring alternative specializations (see text for explanation). Error bars represent 95% confidence intervals.

References

- Annett, C. A., and R. Pierotti. 1999. Long-term reproductive output in western gulls: Consequences of alternate tactics in diet choice. *Ecology* **80**:288-297.
- Beauchamp, G., L. A. Giraldeau, and N. Ennis. 1997. Experimental evidence for the maintenance of foraging specializations by frequency-dependent choice in flocks of spice finches. *Ethology Ecology & Evolution* **9**:105-117.
- Bolnick, D. I., R. Svanback, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist* **161**:1-28.
- Bolnick, D. I., L. H. Yang, J. A. Fordyce, J. M. Davis, and R. Svanback. 2002. Measuring individual-level resource specialization. *Ecology* **83**:2936-2941.
- Bonner, J. T. 1980. *The evolution of culture in animals*. Princeton University Press, Princeton, NJ.
- Boyd, R., and P. J. Richerson. 1996. Why culture is common but cultural evolution is rare. *Proceedings of the British Academy* **88**:77-93.
- Bridcut, E. E., and P. S. Giller. 1995. Diet variability and foraging strategies in brown trout (*Salmo trutta*): An analysis from subpopulations to individuals. *Canadian Journal of Fisheries and Aquatic Sciences* **52**:2543-2552.
- Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**:129-136.
- Chesson, P. L. 1984. Variable predators and switching behavior. *Theoretical Population Biology* **26**:1-26.
- Chittka, L., and J. D. Thomson. 1997. Sensori-motor learning and its relevance for task specialization in bumble bees. *Behavioral Ecology and Sociobiology* **41**:385-398.
- Clark, A. B., and T. J. Ehlinger. 1973. Pattern and adaptation in individual behavioral differences. Pages 1-47 in P. P. G. Bateson and P. H. Klopfer, editors. *Perspectives in Ethology*. Plenum Publishing Corp., New York, NY.
- Clark, C., and M. Mangel. 2000. *Dynamic state variable models in ecology: Methods and applications*. Oxford University Press, New York, NY.
- Croy, M. I., and R. N. Hughes. 1991. The role of learning and memory in the feeding behavior of the fifteen-spined stickleback *Spinachia spinachia l.* *Animal Behaviour* **41**:149-160.

- Cunningham, P. N., and R. N. Hughes. 1984. Learning of predatory skills by shore crabs *Carcinus maenas* feeding on mussels and dog whelks. *Marine Ecology-Progress Series* **16**:21-26.
- Darwin, C. 1876. *The effects of cross- and self-fertilization in the animal kingdom*. Murray, London.
- DiCiccio, T. J., and B. Efron. 1996. Bootstrap confidence intervals. *Statistical Science* **11**:189-212.
- Doak, D. F., and W. F. Morris. 2002. *Quantitative conservation biology: Theory and practice of population viability analysis*. Sinauer Associates, Sunderland, MA.
- Dukas, R. 1998. Evolutionary ecology of learning. Pages 129-174 in R. Dukas, editor. *Cognitive ecology: The evolutionary ecology of information processing and decision making*. University of Chicago Press, Chicago, IL.
- Dukas, R., and C. W. Clark. 1995. Searching for cryptic prey: A dynamic model. *Ecology* **76**:1320-1326.
- Ehlinger, T. J. 1990. Habitat choice and phenotype-limited feeding efficiency in bluegill: Individual differences and trophic polymorphism. *Ecology* **71**:886-896.
- Estes, J. A. 1990. Growth and equilibrium in sea otter populations. *Journal of Animal Ecology* **59**:385-402.
- Estes, J. A., D. F. Doak, J. R. Bodkin, R. J. Jameson, D. H. Monson, J. Watt, and M. T. Tinker. 1996. Comparative demography of sea otter populations. *Endangered Species Update* **13**:11-13.
- Estes, J. A., M. L. Riedman, M. M. Staedler, M. T. Tinker, and B. E. Lyon. 2003. Individual variation in prey selection by sea otters: Patterns, causes and implications. *Journal of Animal Ecology* **72**:144-155.
- Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. *Annual Review of Ecology & Systematics* **19**:207-234.
- Gegear, R. J., and T. M. Laverly. 1998. How many flower types can bumble bees work at the same time? *Canadian Journal of Zoology* **76**:1358-1365.
- Giorni Christopher, J., B. Sinervo, D. Repasky, and T. B. Smith. 1996. Character displacement in two species of Californian lizards as revealed by translocation experiments and studies of resource use. *Bulletin of the Ecological Society of America* **77**:165.
- Golet, G. H., K. J. Kuletz, D. D. Roby, and D. B. Irons. 2000. Adult prey choice affects chick growth and reproductive success in pigeon guillemots. *Auk* **117**:82-91.

- Goulson, D. 1999. Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. *Perspectives in Plant Ecology Evolution and Systematics* **2**:185-209.
- Goulson, D., J. C. Stout, and S. A. Hawson. 1997. Can flower constancy in nectaring butterflies be explained by Darwin's interference hypothesis? *Oecologia* **112**:225-231.
- Guinet, C., and J. Bouvier. 1995. Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology* **73**:27-33.
- Heimlich-Boran, J. R. 1988. Behavioral ecology of killer whales *Orcinus orca* in the Pacific Northwest USA. *Canadian Journal of Zoology* **66**:565-578.
- Heinrich, B. 1976. The foraging specializations of individual bumblebees. *Ecological Monographs* **46**:105-128.
- Heinrich, B. 1979. Majoring and minoring by foraging bumblebees *Bombus vagus* - experimental analysis. *Ecology* **60**:245-255.
- Heinrich, B., P. Mudge, and P. Deringis. 1977. Laboratory analysis of flower constancy in foraging bumblebees: *Bombus ternarius* and *B. terricola*. *Behavioral Ecology and Sociobiology* **2**:247-265.
- Hirvonen, H., E. Ranta, H. Rita, and N. Peuhkuri. 1999. Significance of memory properties in prey choice decisions. *Ecological Modelling* **115**:177-189.
- Hori, M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science (Washington D C)* **260**:216-219.
- Houston, A. I., and J. M. McNamara. 1985. The variability of behavior and constrained optimization. *Journal of Theoretical Biology* **112**:265-274.
- Houston, A. I., and J. M. McNamara. 1988. A framework for the functional analysis of behavior. *Behavioral and Brain Sciences* **11**:117-164.
- Huffman, M. A., and D. Quiatt. 1986. Stone handling by Japanese macaques, *Macaca fuscata*: Implications for tool use of stone. *Primates* **27**:413-424.
- Hughes, R. N. 1979. Optimal diets under the energy maximization premise: The effects of recognition time and learning. *American Naturalist* **113**:209-222.
- Hughes, R. N., and N. O'Brien. 2001. Shore crabs are able to transfer learned handling skills to novel prey. *Animal Behaviour* **61**:711-714.

- Kandori, I., and N. Ohsaki. 1998. Effect of experience on foraging behavior towards artificial nectar guide in the cabbage butterfly, *Pieris rapae crucivora* (Lepidoptera: Pieridae). *Applied Entomology and Zoology* **33**:35-42.
- Keasar, T., E. Rashkovich, D. Cohen, and A. Shmida. 2002. Bees in two-armed bandit situations: Foraging choices and possible decision mechanisms. *Behavioral Ecology* **13**:757-765.
- Kolliker, M., M. W. G. Brinkhof, P. Heeb, P. S. Fitze, and H. Richner. 2000. The quantitative genetic basis of offspring solicitation and parental response in a passerine bird with biparental care. *Proceedings of the Royal Society of London - Series B: Biological Sciences* **267**:2127-2132.
- Krebs, J. R., J. T. Erichsen, M. I. Webber, and E. L. Charnov. 1977. Optimal prey-selection by the great tit (*Parus major*). *Animal Behaviour* **25**:30-38.
- Laverty, T. M. 1980. The flower visiting behavior of bumble bees *Bombus spp*: Floral complexity and learning. *Canadian Journal of Zoology* **58**:1324-1335.
- Laverty, T. M. 1994. Bumble bee learning and flower morphology. *Animal Behaviour* **47**:531-545.
- Laverty, T. M., and R. C. Plowright. 1988. Flower handling by bumblebees: a comparison of specialists and generalists. *Animal Behaviour* **36**:733-740.
- Lefebvre, L. 1995. Culturally-transmitted feeding behaviour in primates: Evidence for accelerating learning rates. *Primates* **36**:227-239.
- Mangel, M., and C. Clark. 1988. *Dynamic modeling in behavioral ecology*. Princeton University Press, Princeton, NJ.
- Mann, J., and B. Sargeant. 2003. Like mother, like calf: The ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops aduncus*). Pages 474 in D. Fragaszy and S. Perry, editors. *The biology of traditions: Models and evidence*. Cambridge University Press., Cambridge, UK.
- McNamara, J. M., and A. I. Houston. 1985. Optimal foraging and learning. *Journal of Theoretical Biology* **117**:231-250.
- Monson, D. H., J. A. Estes, J. L. Bodkin, and D. B. Siniff. 2000. Life history plasticity and population regulation in sea otters. *Oikos* **90**:457-468.
- Neter, J., W. Wasserman, and M. H. Kutner. 1990. *Applied linear statistical models: Regression, analysis of variance, and experimental designs*, 3rd edition. Irwin, Chicago, IL.

- Norton-Griffiths, M. 1968. The feeding behaviour of the oystercatcher, *Haematopus ostralegus*. Ph.D. dissertation. University of Oxford, Oxford, UK.
- Partridge, L. 1976. Individual differences in feeding efficiencies and feeding preferences of captive great tits. *Animal Behaviour* **24**:230-240.
- Partridge, L., and P. Green. 1985. Intraspecific feeding specializations and population dynamics. Pages 207-226 in R. M. Sibley and R. H. Smith, editors. *Behavioral Ecology*. Blackwell Press, Oxford, UK.
- Pulliam, H. R. 1974. On the theory of optimal diets. *American Naturalist* **108**:59-75.
- Railsback, S. F. 2001. Concepts from complex adaptive systems as a framework for individual-based modelling. *Ecological Modelling* **139**:47-62.
- Reiriz, L., A. G. Nicieza, and F. Brana. 1998. Prey selection by experienced and naive juvenile Atlantic salmon. *Journal of Fish Biology* **53**:100-114.
- Rendell, L., and H. Whitehead. 2001. Culture in whales and dolphins. *Behavioral & Brain Sciences* **24**:309-382.
- Riedman, M. L., and J. A. Estes. 1990. The sea otter, *Enhydra lutris*: Behavior ecology and natural history. U S Fish and Wildlife Service Biological Report **90**:1-126.
- Robinson, B. W., and D. S. Wilson. 1994. Character release and displacement in fishes: A neglected literature. *American Naturalist* **144**:596-627.
- Robinson, B. W., and D. S. Wilson. 1995. Experimentally induced morphological diversity in Trinidadian guppies (*Poecilia reticulata*). *Copeia* **1995**:294-305.
- Roughgarden, J. 1972. Evolution of niche width. *American Naturalist* **106**:683-718.
- Schindler, D., J. R. Hodgson, and J. F. Kitchell. 1997. Density-dependent changes in individual foraging specialization of largemouth bass. *Oecologia* **110**:592-600.
- Schmitz, O. J., J. L. Cohon, K. D. Rothley, and A. P. Beckerman. 1998. Reconciling variability and optimal behaviour using multiple criteria in optimization models. *Evolutionary Ecology* **12**:73-94.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology & Systematics* **2**:369-404.
- Sherratt, T. N., and A. D. MacDougall. 1995. Some population consequences of variation in preference among individual predators. *Biological Journal of the Linnean Society* **55**:93-107.

- Shettleworth, S. J. 1998. Cognition, evolution and behavior. Oxford University Press, Inc., New York, NY.
- Smith, T. B. 1990. Natural selection on bill characters in the two bill morphs of the african finch *Pyrenestes ostrinus*. *Evolution* **44**:832-842.
- Smith, T. B., and S. Skúlason. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians and birds. *Annual Review of Systematics and Ecology* **27**:111-133.
- Stephens, D. W., and J. R. Krebs. 1986. Foraging Theory. Princeton University Press, Princeton, NJ.
- Stoinski, T. S., N. Ure, J. Wrate, and A. Whiten. 2000. Observational learning of food processing techniques in gorillas (*Gorilla g. gorilla*). *American Journal of Primatology* **51**:93.
- Stoinski, T. S., J. L. Wrate, N. Ure, and A. Whiten. 2001. Imitative learning by captive western lowland gorillas (*Gorilla gorilla gorilla*) in a simulated food-processing task. *Journal of Comparative Psychology* **115**:272-281.
- Terkel, J. 1996. Cultural transmission of feeding behavior in the black rat (*Rattus rattus*). in C. M. Heyes and B. G. Galef, Jr., editors. *Social learning in animals: The roots of culture*. Academic Press, Inc., San Diego, California.
- Verbeek, M. E. M., P. J. Drent, and P. R. Wiepkema. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour* **48**:1113-1121.
- Visalberghi, E., and E. Addessi. 2001. Acceptance of novel foods in capuchin monkeys: Do specific social facilitation and visual stimulus enhancement play a role? *Animal Behaviour* **62**:567-576.
- Weinrich, M. T., M. R. Schilling, and C. R. Belt. 1992. Evidence for acquisition of a novel feeding behaviour: Lobtail feeding in humpback whales, *Megaptera novaeangliae*. *Animal Behaviour* **44**:1059-1072.
- Werner, E. E., G. G. Mittelbach, and D. J. Hall. 1981. The role of foraging profitability and experience in habitat use by the bluegill sunfish. *Ecology* **62**:116-125.
- Werner, T. K., and T. W. Sherry. 1987. Behavioral feeding specialization in *Pinaroloxias inornata*, the "Darwin's Finch" of Cocos Island, Costa Rica. *Proceedings of the National Academy of Sciences of the United States of America* **84**:5506-5510.
- West, L. 1986. Interindividual variation in prey selection by the snail *Nucella emarginata*. *Ecology* **67**:798-809.

- West, L. 1988. Prey selection by the tropical snail *Thais melones*: A study of interindividual variation. *Ecology* **69**:1839-1854.
- Wildhaber, M. L., and L. B. Crowder. 1995. Bluegill sunfish (*Lepomis macrochirus*) foraging behavior under temporally varying food conditions. *Copeia* **1995**:891-899.

Appendices

Following Pages:

Appendix A. Maximum Likelihood analysis of carcass distributions and population counts

Appendix B. Sea otter survival rates: Maximum Likelihood estimates for 1992-2001

Appendix C. Maximum Likelihood analysis of mark-resight survival data, 2001-2003

Appendix D: Prey biomass and energy content conversion parameters

Appendix E: Summary of Discriminant Analysis Results

Appendix F: Summary of Principal Component Analysis Results

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

<u>Model Support</u>		<u>Model Description</u>							
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 high 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. Sea otter survival rates: Maximum Likelihood model-averaged estimates for 1992-2001

1. Northern Periphery of Range

Year	Juvenile (0-1 years)				Subadult (2-3 years)				Adult (4-10 years)				Old Adult (11-20 years)			
	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95
<u>Females</u>																
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
<u>Males</u>																
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

Appendix B. (continued)

2. North-Center of Range

Year	Juvenile (0-1 years)				Subadult (2-3 years)				Adult (4-10 years)				Old Adult (11-20 years)			
	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95
<u>Females</u>																
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
<u>Males</u>																
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

Year	Juvenile (0-1 years)				Subadult (2-3 years)				Adult (4-10 years)				Old Adult (11-20 years)			
	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95
<u>Females</u>																
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
<u>Males</u>																
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

Year	Juvenile (0-1 years)				Subadult (2-3 years)				Adult (4-10 years)				Old Adult (11-20 years)			
	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95	Mean	SE	L95	U95
<u>Females</u>																
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
<u>Males</u>																
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. Maximum Likelihood analysis of mark-resight survival data, 2001-2003: summary of 10 model forms having greatest support ($\Delta_i \leq 10$)

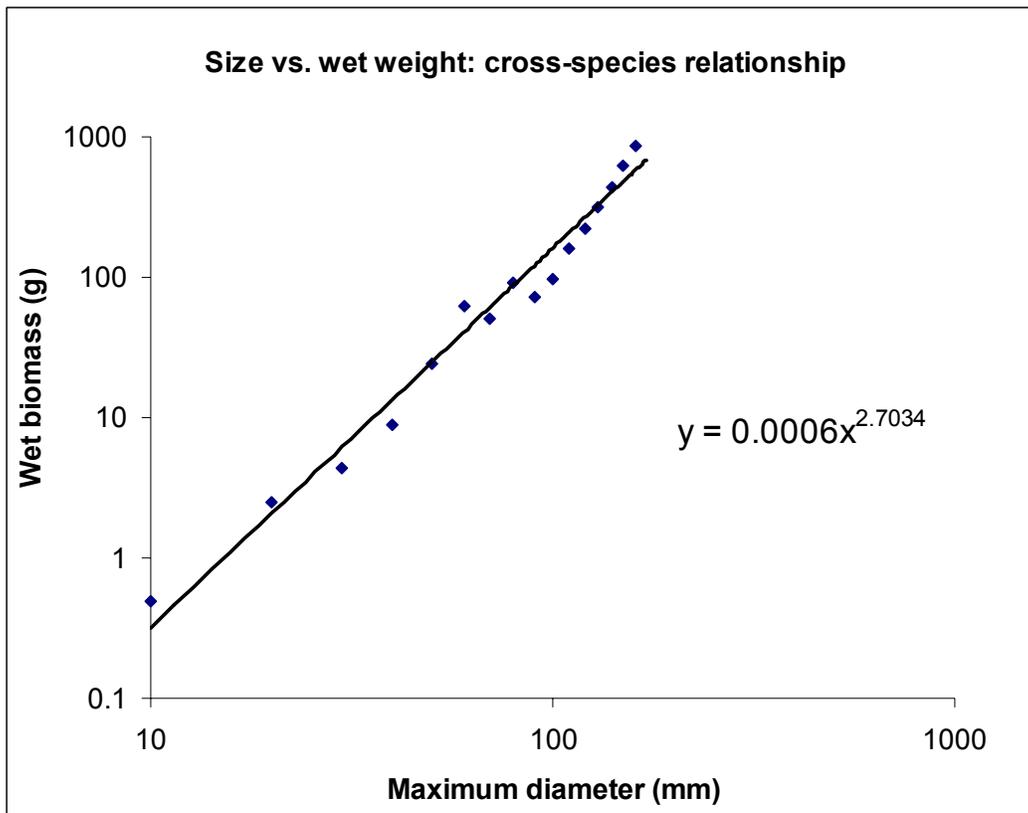
<u>Model Support</u>		<u>Model Description</u>				
AIC	a_i	Sex Effect	Spatial Variation ¹	Yearly Variation	Seasonal Variation	Season-Location Interaction
254.3	0.541	No	(1 = 2) < 3	no	summer < winter & fall in areas 1 & 2	summer > winter & fall in area 3
256.6	0.172	No	(1 = 2) < 3	no	summer < winter & 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: Prey biomass and energy content conversion parameters used for analyses of diet content (by weight) and rate of energy acquisition. Equations to convert prey diameter (mm) to wet edible biomass (g) were taken 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). Note: Referenced literature is cited as numbers in tables, and full citations are provided below.

Species used to derive generalized, cross-species relationship

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



Appendix D. (continued) Mean recorded size (in cm) for each prey type and associated estimated wet edible biomass. Estimated energy content is also shown for each size class, calculated using published size-biomass conversion equations and energy density values.

Prey Type	References	Mean Size (cm)	Mean estimated wet biomass (g)	Energy Content (kJ per item)			
				Size 1 (1-5 cm)	Size 2 10 cm)	(6- Size 3 15 cm)	(11- 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	-	-	-

Appendix D. (continued)

Footnotes:

¹ Not derived from equations because size was impossible to measure. Value represents approximation based on average handling times.

² No published size-biomass conversion calculations were found, and thus the generalized, cross-species relationship (see above) was used for biomass estimations.

Literature cited in tables (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.
2. Dean, T. A., J. L. Bodkin, A. K. Fukuyama, S. C. Jewett, D. H. Monson, C. E. O'Clair, and G. R. VanBlaricom. 2002. Food limitation and the recovery of sea otters following the 'Exxon Valdez' oil spill. *Marine Ecology-Progress Series* **241**:255-270.
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 E: Summary of Discriminant Analysis Results

Prey Type	<u>Standardized Canonical Coefficients</u>			
	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
cephalopod	0.09	-0.054	-0.053	0.107

<u>Group Means</u>	<u>Cluster 1</u>	<u>Cluster 2</u>	<u>Cluster 3</u>
abalone	5.125	1.155	0.259
clam	1.453	4.502	0.710
cancer crab	22.376	7.393	0.975
cephalopod	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

Appendix E. (continued)

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

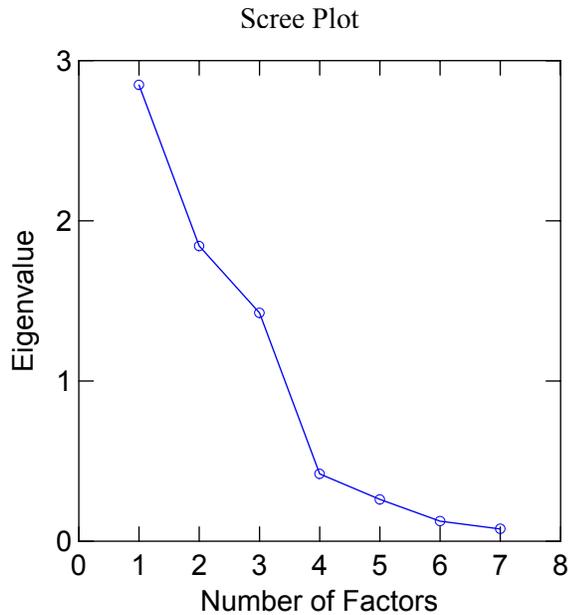
Appendix F: Summary of Principal Component Analysis Results

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 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