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**MORPHOLOGICAL AND BEHAVIORAL CORRELATES OF
POPULATION STATUS IN THE SOUTHERN SEA OTTER, *ENHYDRA*
LUTRIS NEREIS: A COMPARATIVE STUDY BETWEEN CENTRAL
CALIFORNIA AND SAN NICOLAS ISLAND**

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Abstract

I examined the relationship between population density and patterns of behavior and morphology in the Southern sea otter (*Enhydra lutris nereis*) by contrasting the recently established low-density population at San Nicolas Island (SNI) with the long established high-density population in central California (Piedras Blancas, PBLA). One hundred and forty southern sea otters were translocated from PBLA to SNI in 1988-1990. After declining to near extinction, the surviving animals at SNI began to increase in 1993 and the population has since grown at 8.7% yr⁻¹. Currently, the population density at SNI is about 0.33 otters km⁻² whereas the density in central California is about 2.56 otters km⁻². A comparison of these populations and their prey resources thus affords the unique opportunity to examine the effect of intraspecific competition and density-dependence on the behavior and morphology of a large, mobile predator. The mean densities of high quality invertebrate prey were 10³ times greater at SNI than at PBLA, and I found that the mean rate of energy gain by foraging otters also was significantly higher at SNI. As a likely consequence, body condition was better and foraging activity was reduced in sea otters at SNI compared with PBLA. Distinct patterns of individuality in diet and foraging behavior that

characterized sea otters at PBLA were absent at SNI. Dietary niche width was narrower overall at SNI than at PBLA and at SNI we found considerably greater overlap between the individual and population level diets. These data support the hypothesis that food limitation is an important factor in shaping and maintaining behavioral polymorphisms, and lend support to the idea that competition for prey resources is a likely factor contributing to the stalled recovery of the threatened Southern sea otter.

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At every step of the way, the success of this project has been due to the combined efforts of many individuals and agencies. From the very beginning it has been clear that there is a great deal of interest in the San Nicolas Island sea otter population and a sense of excitement that we might be able to take advantage of this opportunity to observe a population as it increases towards carrying capacity. Financial and logistical support was provided by USGS Biological Resources

Division (WERC), California Department of Fish and Game, the Monterey Bay Aquarium (SORAC division), US Navy, US Fish and Wildlife Service, The Friends of Long Marine Laboratory, and UCSC Services for Transfer and Re-Entry Students. My interest in this project was initiated by a trip out to San Nicolas with Brian Hatfield of the US Geological Survey, who has been involved in the translocation project from the beginning and continues to census the population regularly. His enthusiasm and support for beginning a research project on the island was key to its success and his knowledge of the history of the translocation proved invaluable. Additionally, his leadership during the capture efforts was largely responsible for our success in marking and instrumenting so many otters. Greg Sanders, of US Fish and Wildlife Service Ventura Office, has been “ground zero” for much of the controversy surrounding the San Nicolas translocation project and has unfailingly offered his support for the work I have done. Lilian Carswell, also of the Ventura Office, has joyfully contributed to the field work by helping to monitor the San Nic otters while I was writing and was instantly inducted into the exclusive society of sea otters trackers. I am also indebted to Galen Rathbun, who worked on the original translocation effort and (together with Brian Hatfield) made available the foraging data from the early days of this population that proved to be so interesting.

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The capture and instrumentation of sea otters on a remote island requires the help of many skilled individuals and the cooperation of several agencies. Dr. Mike

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Introduction

Top-level carnivores are often limited by the abundance of their prey resource (Estes 1996, Fryxell et al. 1999), and can be expected to undergo shifts in behavior in response to increasing density and the associated reduction of resource availability (Krebs 1978, Sih 1984, Alcock 2001). However, changes of this nature are difficult to document for two important reasons. One is that many top-level carnivores have been extirpated or depleted to low densities and their natural habitats have been substantially altered. The other is that the dynamic relationships are difficult or impossible to infer from descriptions of static systems (May 1973) and prey resource availability relative to predator population density is not easily perturbed for the purpose of scientific study. The comparative approach—i.e., contrasting the behavioral ecology of predators among systems in which their population status and prey resource availability are known to vary—is one practical solution to this dilemma.

The fragmented nature of large carnivore populations today provides abundant opportunities to use the comparative approach. Comparisons across systems in which the density of a predator population is known to vary can provide insight into the functional relationships between behavior and population status (Krebs and Davies 1993). Once these relationships have been established, behavioral indices can be used elsewhere to characterize the status of predator populations and to distinguish trends in population dynamics that may not be apparent from standard measures of

abundance alone. The determination of a species' response to density-dependent processes can shed light on the link between foraging ecology and population dynamics, becoming an important component in the assessment of population health and conservation.

In systems where relative prey abundance defines the linkage between predator abundance and density-dependent processes, studies of foraging ecology can illuminate relationships between behavior and population status. Foraging behavior, an organism's strategy for the acquisition of energy, is tightly linked to survival and reproduction, with fitness being the measure of the strategy's overall performance. The fitness of individuals adopting a particular foraging strategy is thus dependant on the performance of that strategy in the context of the current state (or condition) of the environment

For many apex predators, competition between conspecifics for limited resources is a powerful driver of phenotypic diversification (Bolnick et al. 2003). The extent to which individuals differ in diet consistency and width from the population as a whole can be both density and frequency dependent, such that the types of strategies that are favored depend on the relative frequency of alternative strategies (Skulason and Smith 1995, Schindler et al. 1997, Svanback and Persson 2004). Previous studies have described an increase in individual foraging specialization as pressure from intraspecific competition increases (Collins et al. 1993, Schindler et al. 1997, Bolnick et al. 2003, Svanback and Persson 2004), and changes in the

proportion of daily activity allocated to foraging may also result as food becomes more difficult to acquire (Sih 1984, Mitchell et al. 1990, Gelatt et al. 2002, Cornick and Horning 2003). Individual specialization may occur in the form of foraging polymorphisms that represent discrete, alternative strategies for optimizing foraging success. While such polymorphisms may be associated with morphological or physiological differences (Skulason and Smith 1995), they can also be based solely on behavioral differences (Caraco et al. 1995, Houston and McNamara 1999). The plastic nature of behavioral-based polymorphisms should allow for flexibility in the nature and the speed of an individual's response to change, so that a relaxation of competitive pressure could be expected to result in fairly rapid reversion of multiple behavioral phenotypes to a single strategy.

The sea otter (*Enhydra lutris*) and its coastal marine ecosystem provide an excellent empirical system for exploring how the density of an apex predator affects foraging behavior. Both sea otter diet and prey abundance and composition are relatively easy to observe and quantify as many of the prey are large, sessile or weakly motile organisms and sea otters typically forage close to shore and consume their prey at the ocean's surface. Sea otters also are capable of limiting prey abundance (Estes & Palmisano 1974) and previous studies have linked population density to foraging patterns and dietary change (Estes 1982, Ostfeld 1982, Watt et al. 2000, Estes et al. 2003). In addition, sea otters have undergone dramatic changes in abundance when re-colonizing areas where they have long been absent, affording the

opportunity to examine not only the effect of a predator on its community, but the effect of increasing intraspecific competition on behavior.

The fur trade of the 18th and 19th centuries reduced the sea otter to a few small remnant populations (Kenyon 1969). The southern sea otter (*E. lutris nereis*) is recognized as a subspecies and currently ranges from northern California to just south of Point Conception (USGS unpublished survey data). In 1973, the southern sea otter was listed as threatened under the Endangered Species Act due to the population's small size, limited distribution and perceived vulnerability to contamination by a catastrophic oil spill (Van Blaricom and Jameson, 1982). Since attaining protected status in 1911, the remaining southern sea otter population has grown to roughly 2500 animals (USGS unpublished survey data, spring 2004), and has not increased at a rate greater than 5% per year during the subsequent recovery period (Estes et al. 2003a), a rate well below the estimated r_{\max} ¹ for sea otters of about 20% per year (Estes 1990, Riedman and Estes 1990, Estes et al. 2003b). For reasons that have yet to be clearly understood, a period of population decline began in the 1990s, with annual counts decreasing between 1995 and 1999 (Estes et al. 2003b, USGS, unpublished survey data). Since that time, growth has been greatly depressed and has, in effect, ceased in range-center regions (USGS, unpublished survey data). These periods of slow growth and decline of the California population have been attributed to elevated mortality rather than reduced fecundity, with a relatively high percentage of beach-cast carcasses consisting of prime-age adults (Estes et al. 2003a, Gerber et al. 2004),

¹ R_{\max} estimate is based on age of first reproduction, annual birth rate of females and age of last reproduction. This estimate of r_{\max} has been realized in some recovering populations.

and more specifically, prime-age females (Estes et al. 2003a, Tinker 2004). Emerging parasitic diseases, for which the sea otter is not the definitive host, have been the proximate cause of death in a large proportion of carcasses collected since the 1990s (Estes et al. 2003a, Kreuder et al. 2003, Jessup et al. 2004). These pathogens are thought to be more or less independent of sea otter density, as they are hypothesized to be linked to contamination of nearshore habitats and are not known to be directly transferable between sea otters (Kreuder et al. 2003, Jessup et al. 2004). However, long term declines in body condition and foraging success also have been seen in the last decade (Estes et al. 2003a, Tinker 2004) and what remains unclear is the extent to which density-independent factors, in this case parasitic diseases, interact synergistically with density-dependent factors such as food limitation to limit population growth. For example, nutritionally stressed otters are potentially more susceptible to disease, and an increasing dependence on secondary (i.e. less energetically profitable) prey items that are known bio-accumulators and vectors of pathogens may increase the probability of exposure to disease (Kreuder et al. 2003, Jessup et al. 2004).

The California coastline, while representing only 25% of the available land mass for the state, is home to > 75% of the state's population (Kildow and Colgan 2005). As a consequence of this high human density, coastal habitats have been heavily influenced by a variety of human activities (i.e. commercial fisheries, pollution and recreation) during the sea otter's period of recovery, likely contributing

to a reduction in densities of benthic invertebrates which in turn may limit sea otter population growth and, ultimately, the potential equilibrium density. Long-term studies have been conducted in Monterey Bay and central California, characterizing trends in demography and foraging ecology (Ralls and Siniff 1990, Estes et al. 2003b, Tinker et al. 2004). Both of these California study areas have been occupied by sea otters at high densities for more than 30 years, and densities of preferred prey items have been affected by intense predation (Estes and Reidman 1990, Ebert 1968). It has been hypothesized that food limitation could be driving the emergence of alternative foraging polymorphisms and may be a factor contributing to the slow growth of the California population (Estes et al. 2003b, Tinker et al. 2004). Additionally, sea otter body condition (Monson et al. 2000, Dean et al. 2002, Laidre et al. unpublished data) and activity budgets have been linked in previous studies to population status and may prove to be reliable indicators of food limitation. However, these density-related hypotheses are difficult to evaluate based exclusively on the study of sea otters in central California for the simple reason that dynamic processes are difficult to evaluate through examination of static “snapshots” of a system. Comparative data are needed from a similar system in which sea otters were either known to be at or near equilibrium density, or far below equilibrium density.

An opportunity does exist to contrast sea otters in central California with a comparable system in which sea otters are far below equilibrium density. From 1987-1990, in an effort to create a “buffer” population against the threat of a catastrophic

event, sea otters were translocated to San Nicolas Island, the most remote of southern California's Channel Islands. This island provides seemingly ideal habitat for sea otters and lies within the species' historic range. After an initial post-translocation "settling" period during which the population dropped to a minimum level (USGS unpublished survey data), the San Nicolas population has grown at a rate of just under 9% per year (Figure 1) which, while still below the aforementioned estimated r_{\max} of about 20% per year, is still considerably greater than the average growth rate of the mainland population. The sea otter population at San Nicolas Island is very likely well below carrying capacity. A longitudinal survey of subtidal and intertidal invertebrates has been underway at San Nicolas since just prior to the translocation effort, and this long-term data set provides a wealth of information regarding trends in the abundances of the sea otter's invertebrate prey. Data from foraging observations made on the island during and subsequent to the translocation effort are also available, and these allow examination of how behavior may have changed as descendants of the newly relocated otters adjusted to more plentiful resources. Comparable data on prey abundance and sea otter foraging behavior are available from central California.

The primary objective of my study was to compare resource abundance and three resource-related indices--body condition, foraging behavior, and time-activity budgets--between the low-density sea otter population at San Nicolas Island and a higher-density population from central California. If food availability varies between

these two sites, then body condition should vary accordingly, with San Nicolas sea otters showing better body condition than those from the central California site. If foraging specializations seen in the central California population are indeed a response to increasing intraspecific density, they should be absent in a low density population and I predict that sea otters at San Nicolas Island will show little inter-individual dietary variation. Finally, the activity investment required for baseline energy intake is likely to fluctuate with varied levels of food availability and I expect that sea otters at San Nicolas Island will spend less time feeding than those in central California. If the central California population is truly food limited and if food limitation is indeed manifested in altered body condition and behavior, then substantial differences should be apparent for all three characteristics. The broad goal of my study is to evaluate these hypotheses.

Methods

Study sites

San Nicolas Island (SNI) lies among southern California's Channel Islands, approximately 110 km due west of Los Angeles (Figure 2). It was selected by the U.S. Fish and Wildlife Service as a translocation site for sea otters because of its isolation and an abundance of apparently suitable habitat (USFWS 1987). One hundred and forty sea otters were moved to the island from the central California coast during the 1987-1990 time-period. Concurrently, a sea otter management zone was established that was defined as the coastline from Point Conception to the Mexican border including all of the Channel Islands except for San Nicolas. Containment of the experimental translocated population was to be maintained by the capture and relocation of otters found within the management zone. By the end of 1990, only 15 of the 140 translocated otters remained at San Nicolas and the translocated population reached a low of 12 independent animals in 1993. Unexpectedly high rates of emigration (36 are known to have returned to their home sites), removal from the management zone and mortality from a variety of sources accounted, in part, for the low number remaining at the island (USFWS 2003). However, the population has subsequently grown at a rate of 8.9% (Figure 1), and by 2003, when my study began, it contained 30 independent animals (Brian Hatfield, USGS unpublished survey data).

I determined sea otter density at SNI by dividing the mean population

estimates for study period (2003-2004) by the available suitable habitat, with suitable habitat defined as the area of the subtidal benthos, from the coastline to the 40-m bathymetry line (Laidre et al. 2001, Kage 2004). In order to characterize prey availability at San Nicolas Island, I used information obtained during semiannual subtidal surveys of benthic invertebrates conducted by the USGS, which included counts from 5 permanently marked 20 m² plots at each of 5 survey sites (Table 1). Species selected for analysis were red urchin (*Strongylocentrotus fransiscanus*), purple urchin (*Strongylocentrotus purpuratus*), wavy turban (*Lithopoma undosa*) and red and pink abalone (*Haliotis rufescens* and *H. corrugata*). While this is not an exhaustive list of sea otter prey, these species were selected due to their ubiquity in southern sea otter diets as well as the availability of comparable density data from the central California study area.

The data were compared to similar information obtained in 2001-2004 from the San Simeon/Cambria region of the central coast (hereafter referred to as Piedras Blancas study area, or PBLA), near the center of the sea otter's range in California. The PBLA study site comprised the stretch of coastline between Piedras Blancas and Cayucos, with the majority of data collected between Point San Simeon and Point Estero. This site was re-colonized by sea otters in the mid 1960s (Ebert 1968, Riedman and Estes 1990) and persists at a relatively stable mean density of 2.56 otters/ km² (Kage 2004). Invertebrate prey density for this study area was characterized from data gathered at 3 sites (Table 1) surveyed during 2002-2003 as

part of the subtidal monitoring program of the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO, unpublished data). Invertebrate densities were based on counts from 2-4 30m x 2m plots per site at depths of 5, 12.5, and 20m. I averaged densities across years, sites and depths, with means standardized for variation in number of swaths surveyed per site. From this database, I selected data on prey species comparable to those measured at SNI (in particular the congeneric red turban snail-- *Lithopoma gibberosum*—replaced the wavy turban snail, and pink abalones were absent from central California). Sites sampled were all representative of areas frequented by sea otters (Kage 2004, USGS unpublished survey data) and all depths sampled were within their foraging range (Bodkin et al. 2004, Tinker et al. 2004).

Capture

In October of 2003, 16 sea otters were captured at SNI, tagged with color-coded flipper tags and instrumented with intraperitoneal VHF radio transmitters (Advanced Telemetry Systems, Isanti, MN; projected battery life of 1 year) and time-depth recorders (TDR; Model Mark IX, Wildlife Computers, Redmond, WA). Otters were captured in specially designed “Wilson Traps” by divers equipped with self-contained re-breathers and were transported to shore facilities for surgical implantation of the instruments by a veterinary team. In the month following the capture effort 2 juvenile males that were dependent at the time of capture were weaned. They were both sighted post-weaning at an offshore reef known as ‘The

Boilers', but subsequently disappeared. The fate of these juveniles remains undetermined. Premature failure of the radio implants resulted in sporadic monitoring of an additional 3 otters in the latter half of the first year. In October of 2004, 5 of the implanted animals were recaptured and their TDRs were removed. An additional 5 new otters were tagged and implanted with transmitters but no additional TDRs were deployed.

As part of a complimentary study (Tinker 2004), 60 sea otters from the PBLA study area were captured and instrumented, using identical methods, between spring of 2001 and fall of 2003 (Table 2).

Body Condition

Measurements of body morphometry, in this case mass and body length have previously been utilized as an index of body condition in sea otters (Monson et al 2000, Dean et al 2002). Body mass and body length measurements for sea otters from San Nicolas Island (SNI) and central California (PBLA) were obtained at the times of capture--fall of 2003 and 2004 at SNI (9 females, 10 males), and between January of 2001 and October of 2002 at PBLA (27 females, 8 males) (Table 3). Sex determination, visual age estimation (based on grizzle, size and tooth wear) and measurements of mass and length (linear: from nose to the tip of the tail bone) were taken after the animals were anaesthetized and prior to the implantation procedure. A premolar tooth was extracted whenever possible in order to subsequently estimate age by counting the number of cementum layers (Bodkin et al. 1997). Plotting the visual

age estimates against the tooth estimates showed a linear relationship ($R^2 = 0.61$), and visual age estimates were substituted in cases where tooth age estimation was impossible.

In addition, health exams were carried out on all captured sea otters from both study areas. Blood samples were collected and are currently being analyzed. Subcutaneous fat was noted by veterinary staff to be abundant in most SNI otters, in contrast to PBLA animals that typically have little or no fat reserves (Mike Murray, pers. comm.). As no standardized method for quantifying body fat has been utilized consistently in previous sea otter studies, quantification of the difference in subcutaneous fat is not possible at this time. Dental exams were conducted on all individuals and digital photos taken of both upper and lower jaws in order to document tooth condition and wear.

Mass/length ratios for both sexes were compared between SNI and PBLA using ANOVA. Additionally, body condition was characterized by mass and length at age by using the von Bertalanffy growth equation: $A_{\infty}(1 - e^{-k(t-t_0)})$, where A is asymptotic size, k is a growth rate parameter, and t_0 is the age at which asymptotic growth is achieved (Appendix A). As one of my goals was to better understand the relationship between body condition and population status, the growth data from SNI and PBLA were compared with similar data obtained from populations at well-characterized levels of density in the Aleutian Islands — specifically, from Amchitka Island during the 1967-1971 period, when the population was at or near equilibrium

density; and from Amchitka and several other nearby islands during the 1992-1997 period, when these populations had been reduced (purportedly by killer whale predation; Estes et al. 1998) to levels well below equilibrium density (Laidre et al. *in review*) As the sub-specific status of the southern sea otter in relation to the Aleutian Islands (northern) sub-species (*Enhydra lutris*) is based primarily on differences in skull morphology and geographic isolation (Riedman and Estes 1990), I determined comparisons of mass and length between the sub-species to be valid. The growth curves in each case define the expected mass or length at age (t). To contrast the growth curves among each of the four populations (SNI, PBLA, Aleutian Islands 1960s/1970s, Aleutian Islands 1990s), I compared the deviations (residuals) of the SNI and PBLA growth data around the two growth curves from the Aleutian Islands. In all cases, I plotted sexes separately, as sea otters are sexually dimorphic. I compared the residuals from each population to the growth curves (mean = 0) with a one-tailed, one sample t-test. Additionally, I compared all residuals (mass and length) between the SNI and PBLA populations using two-factor ANOVA to account for potential interaction between study area and sex.

Foraging Behavior

Instrumented otters were located on a daily basis using standard telemetric techniques and those that were found foraging were targeted for observation. Foragers were located visually with a 30X spotting scope (Questar Inc.) and data were collected until the otter finished feeding or visual contact was lost (the data from this

bounded period comprise a foraging “bout”). Data collected included date and time, dive location, duration of dive, duration of surface interval, success (prey capture), prey identification, quantity and size of prey, handling time, tool use, pup provisioning, and weather conditions. Prey items were identified to the lowest possible taxon, and were classified as “unknown” when no identification could be made. Data were collected intensively from November 2003 through September 2004. Every effort was made to randomize bout selection, but due to the shore-based nature of the observations, there was an unavoidable bias towards near shore (<1 kilometer from shore) bouts as well as bouts collected during fair weather months. I was able to collect consistent foraging data on eleven of the original sixteen SNI study animals (Table 2) for a total of 170 bouts (~5000 known-outcome foraging dives). All 11 study animals had > 200 known outcome foraging dives recorded, with >300 dives recorded for all but 1 of these. Foraging data were collected in each of 3 designated “seasons” for 8 of the 11 individuals. This data set was compared to data from the PBLA study (60 otters, 850 bouts, ~34,000 known-outcome foraging dives), which were collected by identical methods between January 2001 and April 2004 (Tinker 2004).

Data collected during and immediately subsequent to the translocation effort provided another point of comparison, allowing a contrast of foraging behavior between recently relocated sea otters and those that had become “naturalized” for over a decade. These data were collected on SNI by USFWS personnel from

September 1987- December 1990 by methods identical to those described above. I restricted further analysis to a sample of 12 individuals for which > 100 known outcome foraging dives had been recorded (Table 2).

I calculated diet composition for SNI as the proportion of each prey item in the overall diet, which I assessed by relative frequency of occurrence of each prey type on feeding dives as well as its relative contribution to consumed biomass. For all analyses pertaining to specialization, I combined similar prey items into 13 categories corresponding to ecological functional groups (Table 4), in a manner consistent with previous analyses (Tinker 2004). All prey items were examined for seasonal variation in percent occurrence in the diet. The population level diet summaries for PBLA and the “Old” SNI population were calculated by identical methods. As dietary niche-width has been known to fluctuate with varying levels of intraspecific competition (Bolnick et al. 2003), I used a Shannon-Weaver function (Shannon and Weaver 1949) to assess and contrast dietary diversity between the 3 populations:

$$H = -\sum p_i \ln p_i \quad (1)$$

with H being the diversity index for the diet of the population, and p_i being the relative proportion of prey item i in the diet. To measure the extent of dietary overlap between SNI individuals and the population, I will calculate a proportional similarity index (PS, Bolnick 2002, Feinsinger et al. 1981) for each individual otter, i :

$$PS_i = \sum_{j=1}^J \min(p_{ij}, q_j) \quad (2)$$

where p_{ij} is the proportion of prey type j used by individual i and q_j is the proportion of the prey type j in the population's diet. PS_i values were then averaged across individuals to estimate a representative PS index for the San Nicolas population. The PS index measures the degree to which individual diets diverge from the population-level diet: if an individual's diet overlaps almost perfectly with the population diet, the PS_i value will approach 1 (Bolnick 2002). I chose this particular index in order to provide estimates of individual resource specialization directly comparable to other taxa (Schindler et al. 1997, Svanback and Persson 2004) and to the central California sea otter population (Tinker 2004). Although PS values for the PBLA study site were calculated using prevalence of prey by biomass (Tinker 2004), this metric proved unreliable for the current data set because the smaller sample sizes resulted in values that were highly skewed by the occurrence of a few rare but very large prey items. Instead, PS values for SNI study animals were calculated on the basis of percent occurrence of prey items in the diet as this approach produced more reliable estimates (i.e. more robust to outliers). Recalculation of the PS index for the PBLA study site using percent occurrence (instead of percent biomass) produced no significant difference in PS estimates. I also calculated the PS index for the "Old" (1988-90) SNI population. All estimates were derived using a bootstrap approach (Quinn and Keough 2002), in order to account for the unbalanced sample sizes (SNI, $n = 11$; PBLA, $n = 32$): specifically, 10 individuals were sampled (with replacement) from each population, the PS indices were calculated, and then this process was repeated

1000 times resulting in estimates of mean PS, variances and 95% confidence intervals for each population. Single factor ANOVA was used to test for significant variance among PS values across all 3 populations, followed by *a priori* planned comparisons (Quinn and Keough 2002) to test for differences between specific pairs of populations.

Multivariate analyses have revealed that individual sea otter diets in central California tend to fall into one of three distinct prey specializations (designated as types 1, 2 and 3; Tinker 2004). To evaluate whether alternate diet specializations occurred at San Nicolas, I used hierarchical cluster analysis to look for similar patterns in the relative abundance of prey types in individual diets. All 13 prey categories used for the central California analysis (Tinker 2004) were retained for this analysis, although 3 of the categories were not observed in any SNI foraging bouts, and individuals from both SNI (n = 11) and PBLA (n = 32) were included. The relative abundance of each prey type in each individual diet was measured in terms of % of total biomass consumed per unit time. I used Pearson's r^2 as the distance measure and Ward's minimum variance method to determine linkage distances. The number of clusters retained as "significant" was determined by graphical examination of the dendrogram and scree plot of join distances vs. number of groups joined (McGarigal et al. 2000). I evaluated the efficacy of the resulting classification (making no *a priori* assumptions about group membership on the basis of population or diet type) using discriminant analysis. In particular, I examined the degree to

which the SNI population: 1) differs from the central California population as a whole and 2) conforms to the previously described pattern of three distinct dietary specializations (Tinker 2004). To test how effectively populations and specialist types were classified by the discriminant analysis scores, I used single-factor ANOVA, making all pairwise comparisons with the Bonferroni correction.

The rate at which individuals acquire energy has often been used as a measure of foraging success in sea otters (Ebert 1968, Costa 1978, Garshelis et al. 1986, Dean et al. 2002). Data collected while observing foraging bouts were used as the basis for determining a mean rate of energy gain (kJ/minute). The following variables were evaluated for each observed feeding dive: 1) success of the dive (whether or not prey were captured); 2) identification of prey item(s) for each successful dive; 3) number of items of each prey type observed; 4) approximate size of each prey item (measured as maximum linear dimension in cm); and, 5) the mean energy content per prey item, which was estimated based on published taxa-specific calorific densities and functional relationships between prey size and edible biomass (Ebert 1968, Costa 1978, Dean et al. 2002, Appendix C). By combining these variables, the energy contents per prey item could be summed across dives for each discrete foraging bout and divided by the duration of the bout in order to calculate a net rate of energy gain (kJ min^{-1}). Unfortunately, due to the observational method used to acquire these data, one or more of these parameters were unrecorded or unknown for some dives. The consequence of simply excluding dives with missing data from analysis would be a

tendency to preferentially exclude dives with shorter surface intervals and/or smaller prey types (as these were more difficult to observe), thereby creating a bias towards successful dives with larger prey types. In order to properly account for the uncertainty associated with missing/unknown variables, I instead utilized a “bootstrap” resampling approach that made use of empirically-derived relationships from observed data to create sampling distributions with which to fill in unknown variables (Tinker 2004). More specifically, this algorithm consisted of the following steps for each of many iterations: 1) bouts were drawn randomly with replacement from the database available for each individual, and further analyses were performed on a dive-by-dive basis for each of these bouts; 2) for dives in which all required data were available, the energy content of each captured prey item was estimated (as described above) and summed for the dive, then adjusted for any items shared with a pup or stolen by another otter; 3) using these known-outcome dives, functional relationships were empirically derived between post-dive surface interval and three dependent variables: i) probability of dive success, ii) number of items captured for each prey type, iii) net energy gain; 4) for dives in which one or more of the dive parameters were missing, the known characteristics of that dive were used to select appropriate values for the missing parameters: for example, if the dive was known to be successful but prey type was unknown, I used the post-dive surface interval to randomly select a value for net energy gain from the appropriate sampling distribution (i.e. based on the empirically-derived relationships specific to that

foraging bout; Tinker 2004); similarly, if the dive was known to be successful and prey type was recorded but the number of items captured was unknown, I used the post-dive surface interval to randomly select a value for number of items from the appropriate sampling distribution; 5) after randomly parameterizing all missing variables as described in step 4, the total energy gain was summed for all dives in the bout and divided by the total duration of the foraging bout to arrive at a mean rate of energy intake in kJ per minute; 6) steps 1–5 were repeated 1000 times for each individual animal. The outcome of this analysis was a set of distributions of mean rate of energy gain (kJ/minute), from which I calculated the long-term average and among-bout variance for each individual. In order to accurately parameterize the model, it was necessary to restrict analyses to a sub-set of 10 individuals for which ≥ 5 bouts with ≥ 15 known outcome dives were recorded. Energy gain estimates (both long-term average rate and between-bout variance) from these 10 individuals were then compared with equivalent estimates from the PBLA study site ($N = 26$; Tinker 2004). Rates of energy gain were log-transformed for normality, and I used two-factor ANOVA to test the significance of effects of study area and sex as well as interaction between the two. Additionally, I tested for an effect due to diet type by contrasting data from all SNI study animals with data for each of the three specialist types at the PBLA study site. To test for an effect due to reproductive status, I utilized data for the 3 adult females from which foraging data had been collected when they were with and without pups, and contrasted rates of energy gain at each

reproductive state using a one-tailed paired t-test, with the prediction that rate of energy gain would be higher in non-reproductive females.

Time-Activity Budgets

If rates of energy gain are indeed higher in non-food limited populations, then foragers should be able to meet their basic energetic requirements in a shorter amount of time. Because sea otters have been characterized as “income” as opposed to “capital” strategists (i.e., they do not effectively store energy (Costa 1993)), it follows that SNI sea otters should allocate a lesser proportion of their daily activity budget to foraging than should individuals in a population that is food limited. In order to test this prediction, two different measures of time-activity budgets were collected and contrasted between SNI and PBLA. First, the continuous dive records obtained from the time-depth recorders were used to estimate the proportion of time spent foraging (Bodkin et al. 2004, Tinker et al. 2004). These estimates were supplemented and “ground-truthed” with data from 12 and 24 hour focal observations in which behavior and activity was recorded at ten minute intervals.

Four of the five recovered instruments included a complete (or nearly complete) data set; however, the data set from one of these was corrupted and was not included in the analyses. One instrument (the adult female) had recorded for just under half of the allotted time of twelve months. Data from 21 TDRs from PBLA had been previously analyzed (Tinker et al. 2004) by methods identical to those described here. As males included in the PBLA data set are known to have split home ranges

with potentially different levels of food availability (Jameson 1989, Kage 2004, Tinker 2004), TDR data from the PBLA males was separated by their location at either the PBLA or the Point Conception (PTCN) study areas. Time-depth data were downloaded, corrected for zero-offset drift, and compiled into distinct dives using Instrument Helper 0.750 (Wildlife Computers, Redmond WA). A minimum dive depth of 1.5 meters (approximately one otter body length) was used in the identification of “significant” dives: this minimum depth requirement for dives is less than that used for previous studies in Alaska (Bodkin 2004) but consistent with analyses conducted using data from sea otters in central California (Tinker et al. 2004). Based on ground-truthing of TDR data (from both SNI and PBLA study animals) against visual observations made during collection of foraging data or 24-hour activity sessions (see below) it appears that the 1.5 m minimum was an appropriate cut-off, consistently and reliably distinguishing true diving activity from artifacts associated with electronic instrument drift or wave motion.

In order to translate the TDR dive records into an activity budgets, it was necessary to distinguish between feeding dives and dives associated with other, non-feeding activity. Foraging sea otters typically dive to the bottom to retrieve prey that is then consumed at the surface, providing measurable dive profile characteristics that can be used to differentiate between feeding and non-feeding dives. These dive profile characteristics were incorporated into a logistic regression identical to that used by Bodkin et al.(2004):

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

where α is a constant and β_i are the slope parameters associated with the independent variables k_i . The independent variables utilized here were dive duration, ratio of bottom time to dive duration (BT/DT), ascent rate, descent rate and two interaction terms: dive duration x ascent rate and BT/DT x descent rate. Both the model form and parameter values were selected based on maximum likelihood test statistics described in Bodkin et al. (2004). The logistic equation calculates a predicted probability for each dive. Dives with $P \geq 0.5$ were classified as feeding dives and dives where $P < 0.5$ were classified as non-feeding encompassing active behaviors such as traveling, grooming and interaction dives (Bodkin et al. 2004, Tinker et al. 2004).

Once all dives on the record were classified as feeding or non-feeding, it was possible to classify behavior at each 10 minute interval over the period of deployment into one of three behavior categories: feeding (feeding dive in progress or had surfaced from a feeding dive within 20 minutes), other active (non-feeding dive in progress or had surfaced from a non-feeding dive within the previous 20 minutes, or resting (not diving, inactive). For each otter from which a TDR was retrieved, I determined the proportion of time (10 minute intervals over a 24 hour period) allocated to each of these behavior categories for each day. Activity budgets were then averaged across the entire record as well as across individuals.

Estimated individual activity budgets derived from TDR data were supplemented by focal animal observations, in which a single selected subject was followed visually for a continuous 12 or 24 hour period (Loughlin 1980, Ralls and Siniff 1990). The majority of these activity “sessions” took place from dawn until dusk, when visual contact with the focal target was lost. Three 24 hour sessions were completed in order to check for consistency between day and night activity budgets, with night time activity being assessed by interpreting characteristic transmission patterns in the telemetry signal (Ralls and Siniff 1990). During these activity sessions, I recorded behavior of the focal animal at ten minute intervals. As with the TDR data analysis, activity was classified into one of three categories: feeding, resting and “other” active (any activity besides feeding). In this way, the proportion of time spent by the focal individual in each activity category for each 12 or 24 hour period was determined. During any 10 minute period in which the behavior of the focal animal was not observed, the behavior was recorded as unknown. As behaviors taking place during these periods could not be reliably categorized as active or inactive they were simply excluded from analysis, and the proportion values for the known behavior categories for each activity session were summed and divided by the corrected total. I excluded from further analysis all activity sessions with $\geq 25\%$ of the 10 minute intervals recorded as unknown.

Using the estimates of percent time feeding based on both methods (TDR data and observational data), I contrasted activity budgets of SNI study animals with

similar data collected at the PBLA study site (Tinker 2004). Due to the great discrepancy in sample sizes from the telemetry-based activity budgets between the two study areas (PBLA $n = 60$; SNI $n = 8$), I determined that comparison of the 95% bootstrap confidence intervals would provide a more robust means of evaluating differences between populations. The bootstrap resampling method was carried out as follows: for each of 1000 iterations, a sample of activity sessions comparable to the SNI sample size was selected with replacement from the data available for each study site, and the proportion of time spent feeding was calculated. From the resulting distributions I estimated the mean and 95% confidence intervals (CIs) for each study area and for the two demographic groups (i.e., males and females) for which I had an SNI sample size of greater than two. Feeding budgets derived from the TDR data were contrasted between populations using a two-sample t-test.

Results

San Nicolas Island includes 98 km² of available sea otter habitat. Based on a mean high count from the USGS quarterly census for 2003-2004 of 32.5 independent sea otters, the estimated population density at SNI is 0.33 otters km⁻², approximately 8 times lower than sea otter densities recorded at the PBLA study site (2.56 otters km⁻²; Kage 2004). Both sea urchins and the *Lithopoma* species were present at SNI in densities that were orders of magnitude higher than PBLA (Table 2, Figure 3); however there was little difference in abalone density between sites.

Body Condition

The simple comparison of mass/ length ratios between SNI and PBLA showed that SNI otters of both sexes are in significantly better condition than otters from PBLA (males: $F = 30.34$, $p \ll 0.001$; females: $F = 22.95$, $p \ll 0.001$; Figures 4 and 5). I hypothesized that sea otters from SNI would be larger (residuals positive) than predicted by a growth curve derived from a representative at-equilibrium population and this was strongly supported by my results (Table 3, Figure 6). Sea otters of both sexes from San Nicolas Island were significantly larger for both mass and length than expected based on the Aleutian Islands 1960s-70s growth curve. Additionally, I expected that PBLA sea otters would be consistent with (residuals = 0) or smaller than (residuals negative) predicted by the at-equilibrium population growth curve. The residuals for mass were consistent with this prediction, but the residuals for length were somewhat surprising (Table 3, Figure 6). Mass residuals for females from

PBLA were significantly smaller than the expected values from Aleutian Islands 1960s-70s, while the mass residuals for males were smaller, but not significantly so. However, when comparing length, both sexes from PBLA were significantly longer when compared to the Aleutian Islands 1960s-70s curve.

The results of the ANOVA for the residuals from the Aleutian Islands 1960s-70s growth curve (Figure 6) showed that the residuals for SNI sea otters were significantly different from PBLA for mass ($F = 51.5$, $p < 0.001$) and length ($F = 37.5$, $p < 0.001$). Predictably, there was an effect of sex on the variance ($F = 18.6$, $p < 0.001$ for length; $F = 22.2$, $p < 0.001$ for mass), but there was no significant interaction between study area and sex ($F = 18.7$, $p = 0.18$ for length; $F = 13.0$, $p = 0.26$).

The growth curves for sea otters at SNI were generally similar with those measured from sea otter populations in the Aleutian Islands that were below equilibrium (Table 3, Figure 4, Figure 5). The SNI sea otters did not differ significantly in mass from the Aleutian Islands 1990s curve (Figure 6). SNI males were significantly longer when compared to the expected values for length, but female lengths did not differ significantly between the populations. Both males and females from PBLA were smaller than the expected values for mass as well as length for the Aleutian Islands 1990s curve (Table 3, Figure 4, Figure 5), although the length residuals for males did not differ significantly.

The ANOVA results for the comparison of the residuals from the Aleutian

Islands 1990s curve between SNI and PBLA, showed that the populations were significantly different from one another for both mass and length ($F = 47.3$, $p << 0.001$ for weight; $F = 48.3$, $p << 0.001$) (Figure 6). In this case, there was an effect of sex on the variance for length ($F = 8.83$, $p = 0.004$), but not for mass ($F = 15.8$, $p = 0.21$), and no significant interaction between study area and sex ($F = 0.69$, $p = 0.41$ for length; $F = 13.3$, $p = 0.25$ for mass).

An unusual pattern of tooth wear was observed in nearly all adults captured at SNI. The condition of the front teeth (upper and lower incisors and canines) was extremely poor, while molars (most often the site of tooth wear in urchin eaters) were relatively normal. Front teeth were broken, cracked, sheared and decayed, and in a few cases entirely absent. This condition was exacerbated in older individuals, but signs of early damage could be seen in sub-adults.

Foraging Behavior

During the 2003-2004 data collection period, the diet of the sea otters on San Nicolas Island was comprised of 13 prey types, and had the lowest Shannon-Weaver diversity value ($H = 1.64$) of the 3 populations analyzed (Table 4). Four prey species (red urchins, kelp crabs, *Cancer* crabs and marine snails (typically, wavy turbans)) accounted for > 90% of the population level diet. Red urchins were the dominant prey type across all seasons (Figure 7) with a peak in consumption in late winter. The proportion of red urchins in the diet was lowest in fall, at which time there was a corresponding peak in kelp crab consumption. Foraging data from the 1988-1990 SNI

population (immediately post-translocation) was also dominated by red urchins, but to a lesser degree than in the current study, and sea otter diets were slightly more diverse at that time ($H = 1.96$) with 9 species making up just under 90% of the total diet. Additionally, the post-translocation diet included a much higher proportion of purple urchins (Table 4) as well as a prey type (sand crabs) that was never observed in the 2003 study. Population-level dietary diversity at PBLA was high ($H = 2.33$) and the diet included 24 different prey types (Table 4). Of the 13 prey types observed at SNI during the current study, 3 were not recorded at significant levels in the PBLA study, resulting in dietary overlap of only 10 species with the central California population.

There was little indication of individual specialization in SNI otters, as indicated by a population PS score (0.82) that was significantly higher than equivalent scores from PBLA ($PS = 0.54$, $F = 37.19$, $p < 0.0001$) and “recently translocated” SNI ($PS = 0.50$, $F = 35.1$, $p < 0.0001$). The bootstrap confidence interval for the PS index at SNI (95% CI = 0.772-0.890) was well above that for the PBLA study site (95% CI = 0.464-0.682). Interestingly, there was no significant difference in PS scores between the current PBLA population and the “recently translocated” SNI population ($F = 1.018$, $p = 0.318$).

The results of a cluster analysis of occurrence of major prey taxa among individual otter diets produced groupings that were generally consistent with previous analyses (Tinker 2004), with 83% of the PBLA individuals clustered within their

expected specialist type². In addition to the three clusters corresponding to mainland dietary specializations, there was a distinct fourth cluster, consisting of 9 of the 11 SNI individuals (Figure 8). The 2 SNI otters that were not included in this fourth group were nested within the mainland “type 1” cluster (large prey specialists *sensu* Tinker 2004), and these were the two individuals with the lowest PSI scores (i.e. the most specialized diets from the SNI study group). Discriminant analysis (DA) confirmed that the four clusters were statistically distinct (Appendix B) and, when superimposed with *a-priori* information on expected group membership (specialist type 1, 2, 3 or SNI), an ordination of the first two DA scores (Figure 9) showed that individuals were generally classified correctly based on diet composition alone. The predominance of red urchins in the diet of SNI otters was the most important factor in their separation from the PBLA diet groups (Appendix B) The two individual SNI females that grouped outside of the SNI cluster had a high proportion of *Cancer* crabs in their diet relative to the other SNI otters, and thus nested within the “type 1” cluster, a grouping driven predominantly by *Cancer* crabs. The effect of study area and specialist type on the first set of discriminate analysis scores was highly significant for all pairwise comparisons ().

Foraging sea otters at SNI had a significantly higher rate of energy gain (49.92 kJ/ min) than did otters at PBLA (33.16 kJ/min, $F = 10.99$, $p = 0.002$) (Table 6). There was no significant effect of sex on rate of energy gain ($F = 0.006$, $p = 0.94$), and no area by sex interaction effect ($F = 1.52$, $p = 0.23$). PBLA types 1 and 2

² The discrepancy results both from the inclusion of data from SNI otters and the exclusion of data from the Monterey Bay study animals.

specialists had significantly lower mean rates of energy gain ($F = 4.88$, $p = 0.035$ for type 1; $F = 14.8$, $p \leq 0.001$ for type 2) than SNI individuals. PBLA type 3 specialists also had a lower mean rate, but the difference was not statistically significant ($F = 1.95$, $p = 0.17$). There was no difference in between-bout variance between study areas overall ($F = 0.001$, $p = 0.979$), but separate contrasts between SNI and diet specialist types at PBLA revealed that between-bout variance of SNI otters was most similar to that of type 1 ($F = 1.17$, $p = 0.20$) specialists at PBLA, and greater than that of type 2 and type 3 specialists ($F = 3.91$, $p = 0.057$). Despite the high between-bout variance at SNI, the probability of exceeding a theoretical “critical intake rate” on any given bout (here defined as 90% of the predicted maintenance costs for an 18 kg female foraging for 65% of the day [Tinker 2004]) was 92%, in contrast to lower probabilities for all of the PBLA specialist types (Figure 10). There was no difference in rate of energy gain in SNI females due to reproductive status ($t = 2.91$, $p = 0.10$), although the limited sample size provided little statistical power to detect an effect.

Time-Activity Budgets

Estimates of time budgets based on the observational (telemetry-based) and TDR data sets were consistent with my prediction that sea otters from SNI would spend less time feeding than those from PBLA (Table 7, Figure 11). The results of the bootstrap analyses show that the means for the telemetry-based estimates of activity budgets in each of the three activity categories differed between the two populations with SNI otters consistently spending less time feeding and more time resting or

engaged in activities other than feeding than otters from PBLA. Based on the observational data, female time budgets differed between populations in all activity categories (Table 7, Figure 11) when analyzed as a discrete demographic group. The sample sizes for reproductive females was too limited for rigorous comparison, but females with pups at SNI fed more overall than non-parous females and their feeding budget differed little from parous PBLA females (Figure 11).

The TDR-based SNI estimates differed from the telemetry-based activity budgets, showing SNI otters spending more time feeding than was expected based on the observational data (Figure 12). Even taking this discrepancy into account, the data from the TDRs showed otters at SNI spent less time feeding than PBLA otters, although the contrast of TDR-based feeding budgets for SNI and PBLA was only marginally significant ($t = 1.94$, $p = 0.08$). The TDR-based activity feeding budget for the single female was consistent with the mean telemetry-based estimate for SNI females, but differed in the amount of time allocated to resting and other active categories (Table 7). The limited sample size did not allow for the TDR data from SNI females to be included as a discrete demographic group in these analyses. The difference in TDR-based feeding budgets for males from SNI and PBLA was negligible until the PBLA males were subdivided by their presence in either the PBLA or PTCN study areas (Table 7, Figure 11). This division showed that males fed less when at PTCN than PBLA, a factor which drove down the overall feeding proportion. Once the results from PTCN were excluded, the TDR based feeding

budgets for PBLA males became more consistent with the observational activity sessions, which had been collected within the PBLA study area. This result lends support to the characterization of the range front as having higher levels of food availability and indicates that the TDR data collected when the males were in the PBLA study area are more appropriate for use in this comparative study. While the extent to which feeding effort differed between SNI and PBLA varied depending on method, my results from both activity budget data sets show that, without exception, sea otters from SNI foraged for a lesser proportion of time than did those from PBLA.

Discussion

The identification of the processes underlying slow population growth or decline in large mammals can be challenging. The translocated sea otter population at San Nicolas Island provides the sort of comparative view necessary to enrich our understanding of sea otter population dynamics within the coastal ecosystem of central California. By examining foraging-related indices such as prey abundance, body condition and behavior and observing how they vary between these populations, it has been possible to better understand the nature, strength and effect of the processes affecting population growth in the threatened southern sea otter.

Prey Availability

Comparisons of prey densities between PBLA and SNI support the conclusion that San Nicolas Island is currently a habitat with nearly unlimited prey resources available to sea otters. Although it was not possible to compare densities of all common sea otter prey species, the four invertebrate categories examined here likely provide a reasonable index of the relative prey abundance at the two sites. Changes in the abundance of preferred sea otter prey species have been documented in the PBLA area as the recovering sea otter population has expanded over the last four decades. Depletion of such prey species as red urchins, abalone and clams is often strongly correlated to the duration of sea otter colonization in a given area, and the presence of sea otters in PBLA has preceded declines in these species (Ebert 1967, Ebert 1968, Wild and Ames 1974). Additionally, the PBLA coastal kelp habitat probably has been

subjected to a variety of human disturbances on a much larger scale than the more remote SNI, with consequences for the invertebrate fauna that range from predictable (the impact of fisheries) to less distinct (pollution).

Of the four prey categories compared between sites, only the abalone species were found in similar densities, a result which was not unexpected as both sites have been subjected to intensive human exploitation (Haaker et al. 2001) and subtidal abalone species have been scarce at SNI for 20 years (USGS, unpublished data). A favored prey item when abundant, abalone did not contribute significantly to the diet of sea otters at SNI, and most were observed as prey items of a single aged female who was a member of the original translocation cohort. The black abalone (*H. cracherodii*), which was not included in the comparisons of prey density, is a primarily intertidal species that has not been commonly observed in previous sea otter foraging studies (Ebert 1968, Ostfeld 1982). It has been severely reduced in number at SNI by withering syndrome (Van Blaricom et al. 1993) but was nevertheless the abalone most frequently observed on SNI as sea otter prey.

The large red urchin, *Strongylocentrotus franciscanus*, is present at SNI in densities several orders of magnitude higher than at PBLA, and was the most frequently observed prey species at SNI. This energy rich organism has previously been documented as a common prey item in re-colonizing sea otter populations and is often among the first species depleted as otter densities increase (Ebert 1968, Estes et al. 1978, Estes et al. 1981). A decline in red urchin abundance on the west end of SNI

has been documented since the mid 1980s (USGS, unpublished data) and surveys conducted since 2000 have recorded numbers at or near zero at this site. This west end region has consistently had the highest densities of sea otters and regions with less sea otter activity have not shown similar declines. Despite these low counts, sea otters acquired red urchins at the west end region regularly during this study and can be assumed to be more adept at locating them than are humans, particularly if the urchins have retreated to crevices. Patterns of sheltering behavior have been documented in red urchins in response to predation (Tegner and Levin 1983, Lee and Estes, unpublished data), and an increase in cryptic behavior could provide a partial explanation for reduced counts. It is not clear, however, to what extent sea otter predation is a factor in these declines. What these data have confirmed is that red urchins, comprising nearly half of the population diet at SNI, are a preferred prey item of sea otters as long as they remain at sufficient levels of abundance.

On average, larger, higher quality prey are acquired in less time (shorter dives) and handled more rapidly by SNI otters than by those from PBLA (Table 8). As a consequence, the rate of energy gain is high at SNI relative to PBLA (Table 6). Individual otters at SNI also had more variation in this rate of energy gain from bout to bout than a typical PBLA otter, but the negative fitness consequences of this variation in energy acquisition at SNI are probably minimal due to the high average rate of energy gain. Sea otters do not typically store energy in the form of fat deposits, and as a result they have little flexibility when it comes to meeting their minimum

energetic demands. Although more variable from bout to bout, the high rate of energy gain at SNI means that these otters have a higher likelihood of meeting (or exceeding) these energetic demands on any given day than do PBLA otters (Figure 10). Indeed, the presence of abundant subcutaneous fat on SNI otters relative to those from PBLA seems to indicate that basal energy intake is often exceeded, creating an additional buffer against the risk of starvation.

Body Condition

Such discrepancies in energy gain between these two populations should manifest in differences in body condition, and my data clearly support this prediction. Mass and length at age of both males and females is substantially greater for otters at SNI than at PBLA. The growth curves of otters at SNI are generally consistent with those computed for Alaska sea otter populations well below equilibrium density (Monson et al. 2000, Laidre et al., in review) whereas the growth curves of otters at PBLA are similar to or even somewhat below those computed for food-limited populations in Alaska (Laidre et al., in review). These data not only demonstrate that body condition is better at SNI than at PBLA, they also lend support to the hypothesis that sea otters in the PBLA area are now significantly impacted by food-limitation (Tinker 2004).

One surprising result was that length at age for SNI otters was equal to or perhaps even greater than that reported for an Aleutian Islands population that was below-equilibrium (Laidre et al., unpublished data). This finding calls into question

the long held belief that the northern sub-species (*E. lutris kenyoni*) is inherently larger than the southern sub-species (*E. lutris nereis*) (Riedmann and Estes 1990). Also somewhat surprising was the amount of subcutaneous fat present on most SNI otters. The 1-2 cm fat layer covering most individuals far surpasses what is typical for southern sea otters (Mike Murray, pers. comm.) and as such may force a reevaluation of generally accepted assumptions about the inability of sea otters to store energy.

With the exception of atypical wear to the front teeth, SNI otters appear to be in good health. A single positive incidence of the protozoal parasite *Toxoplasma gondii* was detected among the individuals captured at SNI. The infection rate for this disease is particularly high in the PBLA region (Kreuder et al. 2003), but no clear relationship between disease prevalence and food availability has been established. Reasons for the poor condition of the front teeth of nearly all of the adult otters captured at SNI is open to speculation. This might be a consequence of the comparatively large and robust prey at SNI or possibly some intrinsic nutritional deficiency or other feature of the SNI environment. Regardless, the poor dental condition of SNI otters does not appear to be compromising their overall health.

Foraging Behavior

One of the most prominent differences between otters at SNI and PBLA concerns the degree of dietary specialization and individuality. At SNI the “within-individual” dietary width overlapped the population-level dietary width by 82%, in contrast to a 54% overlap at PBLA. Individual dietary specialization has previously

been associated with increased intraspecific competition (Collins et al. 1993, Schindler et al. 1997, Bolnick et al. 2003, Svanback and Persson 2004), and this is likely the case for sea otters. These findings imply that where food resources are abundant and competition with conspecifics is minimal, individual otters tend to converge on the one “best” foraging strategy, whereas when food resources are limiting and competition is more intense, individual diets tend to become narrower and more specialized (low within-individual variation) while becoming more diversified at the population-level (high among-individual variation: Estes et al. 2003, Tinker 2004).

The current diet of SNI sea otters is highly typical of those documented for other sea otter populations in the early stages of re-colonization (Ebert 1968, Estes et al. 1978, Estes et al. 1981). The emerging scenario can be summarized as follows: as population density increases at a given location, the preferred prey become depleted or retreat to refugia and the net rate of energy gain begins to decline. Eventually, as energy intake is further reduced, a critical minimum may be reached at which point individuals must either switch to a less preferred but more abundant prey type, or else increase their foraging efficiency with respect to the original “parent” prey type (Krebs 1978, Stephens and Krebs 1986, Gillespie and Caraco 1987, Bateson and Kacelnik 1998, Robinson and Wilson 1998). Recent foraging studies of sea otters in central California indicate that this dietary shift is characterized by individuals adopting one of three distinct and specialized dietary patterns (Tinker 2004). Type 1

specialists typically feed on large prey species (i.e. *Cancer* crabs and abalone) that have low encounter rates and require prolonged handling and/or acquisition times, but provide a high energetic payoff; type 2 specialists consume a variety of medium sized prey items (often species associated with habitats of marginal quality); and type 3 specialists prey almost exclusively on small marine snails (*Tegula* spp.). Of these three diet types, type 2 specialists were most frequently encountered in central California (Tinker 2004). The analyses I present here indicate that this pattern remains intact when data from SNI study animals are combined with data from PBLA. The distinct cluster formed by the SNI otters clearly demonstrates the unique nature of their diet and, by contrast, the extreme dietary diversification that has taken place in the PBLA population. The type 3 (snail) specialists are the most distinct grouping, with just one individual data point transitional between the type 3 grouping and the other clusters. Interestingly, this single point represents a female with preferences for snails as well as large *Cancer* crabs, and may be representative of a transition from one foraging strategy to another. The two SNI females that nested within the PBLA type 1 group had the most diverse diets observed in that study area, and their placement among this specialist type was probably driven by the relatively high proportion of prey types other than urchins (particularly *Cancer* crabs) in their diets.

I suggest that San Nicolas otters exemplify one extreme in a continuum of responses to increasing conspecific densities. The foraging habits of sea otters along

the central California coast have been monitored since the first years of re-colonization, and the cumulative results of current and previous studies place this population progressively farther down this response trajectory (Ostfeld 1982, Estes et al. 2003, Tinker 2004). The extent to which foraging behavior differs between the newly established, low density SNI and the long established, high density PBLA provides perhaps the strongest evidence to date for the existence of nutritional limitation in the California sea otter.

Time-activity Budgets

Time-activity budgets have been extensively studied in sea otters (Estes et al. 1986, Garshelis et al. 1986, Ralls and Siniff 1999, Gelatt et al. 2002). Because sea otters are “income” as opposed to “capital” strategists (i.e., they do not typically have significant energy reserves; Costa 1993), it is necessary for them to increase the proportion of daily time allocated to foraging in order to reach a minimum benefit threshold when prey density becomes reduced. As with patterns in foraging behavior, previous studies of populations in various stages of equilibrium have defined a clear trajectory of increasing foraging effort as populations grow toward carrying capacity (Estes et al. 1986, Garshelis et al. 1986, Giles 1992, Gelatt et al. 2002). Both the telemetry and the TDR-based activity budgets are consistent with this pattern, with SNI at the low end (well below equilibrium density) and PBLA animals foraging for a much higher proportion of time (comparable with other populations thought to be at or near carrying capacity; Tinker et al. 2004). Some discrepancy between the

telemetry and TDR-based activity budgets was apparent for the SNI sample and was likely associated with 1) the inability to detect some types of feeding activity (i.e. kelp canopy foraging) using TDR data alone; and 2) the “snapshot” nature of telemetry-based activity sessions, which (in conjunction with a small sample size) makes these estimates subject to biases due to short-term temporal fluctuations in activity. Future refinement of analysis methods that define the relationship between TDR records and observational data will be useful in resolving these discrepancies; nonetheless, it seems clear from both methods that foraging effort of SNI animals is much lower than that of PBLA animals. A previous study comparing activity budgets between SNI and Big Sur otters found no significant differences in activity budgets (Giles 1992), but these data were collected on SNI in 1988 and 1989, while the translocation effort was in progress. The newly translocated otters may have required more time to become “naturalized” to the novel environment and this may have resulted in a behavioral time lag until such things as prey acquisition skills and body condition “adjusted” to the greater food availability at SNI.

A potentially confounding factor in the evaluation of activity budgets on San Nicolas Island is the higher mean ocean temperature (15.5°C for 2003-2004, Coastal Data Information Program, Historic Data; vs. 13.5°C for PBLA for 2001-2004, USGS unpublished data). The high metabolic rate of sea otters is tightly coupled to the demands of living in a cold water environment (Costa 1978), and patterns of foraging, grooming and resting have been found to be linked to changes in body temperature

(Yeates et al. 2004). The future analysis of records of body temperature recovered from the SNI time-depth recorders in combination with metabolic data will potentially reveal how higher sea temperatures affect sea otter metabolism and activity. A reduction in energetic requirements due to increased sea temperature may be responsible, in part, for reduced levels of feeding activity. However, the high rate of energy gain in the SNI population relative to PBLA, a factor clearly linked to food availability, is likely the most powerful driver of the variation in time-activity budgets between these areas.

Implications

Beyond the quantifiable effects of intraspecific density on morphology and behavior described above, the contrasts I have made between these two sea otter populations have revealed patterns with potentially exciting implications. The relative placement of two populations, SNI and PBLA, along a continuum of increasing intraspecific competition, leads to new insight into the mechanisms underlying behavioral response to environmental variation. The characterization of strategies that are advantageous for each state of density-dependence opens the door for speculation about the dynamic processes that link the two populations together.

The non-random organization of foraging specialization seen in PBLA otters is of particular interest in relation to the single strategy favored at SNI. Similarities of foraging characteristics such as mean success rate, energy rate distributions and prey size selection (Table 8) between SNI otters and the PBLA type 1 (or large prey)

specialists make the type 1 strategy seem most closely related to a “parent” or basal foraging strategy. This trend is illustrated by the similar frequency distributions of rate of energy gain for the SNI and PBLA type 1 specialists (i.e., both have a high mean rate of energy gain that is accompanied by a high variance of this rate (Figure 10). If the sea otter population at SNI continues to grow and intraspecific competition increases, I would predict the SNI energy rate distribution to increase in variance while simultaneously undergoing a directional shift toward lower values and thus an increased probability of falling below the “critical point” corresponding to negative energy balance. This trend should eventually lead to diet diversification and the appearance of alternative specialist types that minimize risk by choosing more abundant but lesser quality prey types. Individuals specializing on less profitable prey types would be expected to maximize energy gain by increasing foraging efficiency (Stephens and Krebs 1986, Bateson and Kacelnik 1998, Houston and McNamara 1999, Doebeli and Dieckmann 2000).

When morphologically or behaviorally diverse prey items require distinct handling or hunting techniques to process or obtain efficiently, specialization represents a trade-off in which a dietary specialist becomes highly skilled at handling (or searching for) one kind of prey at the expense of its ability to feed efficiently on other types (Robinson and Wilson 1998, Bolnick et al. 2003, Estes et al. 2003, Tinker 2004). Behavioral-based polymorphisms, as with morphological polymorphisms, represent fitness “peaks” on an adaptive landscape, with each peak representing a

particularly successful combination of diet composition and foraging skills (Sinervo and Svensson 2002). The fitness “valleys” between the peaks act to limit the tendency of individuals to switch frequently between alternative prey types. Such a process might explain the “behavioral inertia” seen in the newly translocated otters at SNI: the degree of dietary specialization among those transplanted individuals closely matched that which presently occurs in the mainland population from which they were relocated. Additionally, four of the newly transplanted individuals fed on large numbers of mole crabs, a prey type of low nutritional content (based on known values for other crab species in a similar size range, Costa 1978) associated with areas of marginal foraging quality. All of these mole crab foragers were originally captured in the vicinity of Morro Bay (USGS, unpublished data), an area with a high density of sea otters (Laidre et al. 2001, Kage 2004, Brian Hatfield, USGS semi-annual census) and extensive sand-bottom habitat with abundant mole crabs. Specialization by translocated otters on this infaunal species at San Nicolas may have precluded them from taking full advantage (at least initially) of the abundant, higher quality resources in the new and unfamiliar environment. In spite of this behavioral inertia, however, the initial anachronistic prey preferences did not persist over generations, a fact that illustrates the plastic nature of behaviorally-mediated foraging polymorphisms (Alcock 2001). In contrast to genetically-fixed polymorphisms, behavioral polymorphisms based on differences in prey-specific foraging skills are capable of rapid (within-generation) change, allowing an individual to respond to perceived

changes in its environment by acquiring new strategies (Robinson and Wilson 1998). My data suggest that a diverse group of foragers transplanted from an environment with high intraspecific competition has, within a short period, converged upon a single strategy in the face of almost unlimited resources.

Conclusions

The translocation of sea otters to San Nicolas Island was intended as a safeguard against the extinction of the southern sea otter. On that account, this experiment has failed, at least in the time frame originally projected. What this population has provided is an opportunity to view the interrelationship between sea otters and their environment from a dynamic perspective, specifically to document the behavior of sea otters in an unsaturated environment. This fortuitous situation has allowed for the critical detection of inter-population and inter-ecosystem contrasts, a situation that has previously not been possible for the California sea otter. On all accounts, the differences between the San Nicolas and central California populations can be related to increasing sea otter density and the concurrent competition for limiting resources. The characterization of the current mainland population as food-limited at its current level has profound implications for the conservation of sea otters as well and for understanding the overall health of the coastal kelp-based ecosystem with which they are tightly linked. Coastal California is estimated to have supported some 16,000 sea otters prior to the fur trade (Laidre et al. 2001), but anthropogenic alterations to the coastal habitat have likely made these historic numbers impossible

to realize. Density-independent factors such as disease, pollution and incidental fishing gear mortality have been proposed to varying degrees as important factors in the stalled recovery of the California sea otter. These are all undeniably causes of mortality, but the interaction between these factors and the density-dependent reduction of food resources has been a source of some debate. My results provide evidence that food resources are indeed a limiting factor for the high density sea otter population in central California, thus raising the possibility that food limitation is ultimately responsible for the current lack of population increase, or (more likely) that density-dependent food limitation and other mortality factors (such as disease) are inextricably linked.

There are few examples of apex carnivores that have not suffered a dramatic reduction in effective population size in the last century. The often patchy and variable nature of predator populations today may make this kind of comparative study between populations with different levels of predator density more viable and the recognition of opportunities for comparative contrasts vital. As human-caused alterations to the environment continue to increase in magnitude and complexity, it will inevitably become more difficult to isolate the factors responsible for limiting or reducing predator populations. Examination of static populations may not be enough to thoroughly understand the dynamic processes in question: comparative studies offer a potential to yield more complete and compelling answers to questions concerning the response of organisms to a changing environment. As a result, inter-

population contrasts of the sort I have used here will be invaluable for characterizing populations, developing plans for restoration and assessing the progress of recovery plans.

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Tables

Table 1 Methods for invertebrate surveys of central California and San Nicolas Island regions

	San Nicolas Island*	San Simeon/ Cambria**
Survey Site	Nav Fac West End West Dutch Harbor East Dutch Harbor Daytona Beach Sandy Cove	Point San Simeon Cambria Rock White Rock
swath size	20 m ²	60 m ²
# transects per site	5	12***
Survey data used	2000-2004	2002-2004
Species Selected	<i>Strongylocentrotus purpuratus</i> <i>Strongylocentrotus franciscanus</i> <i>Lithopoma undosa</i> <i>Haliotis corrugata</i> <i>Haliotis rufescens</i>	<i>Strongylocentrotus purpuratus</i> <i>Strongylocentrotus franciscanus</i> <i>Lithopoma gibberosum</i> <i>Haliotis rufescens</i>

*US Geological Survey semiannual subtidal surveys

**PISCO subtidal monitoring program

***4 swaths at each of 3 subtidal depths: 5,12 and 20 m.

Table 2 Characterization of three population studies by sea otter density, prey density and sample sizes.

Study Area	Otter Density / km ²	Selected Invertebrate Prey	Mean Density /m ² (SD)	Years of Study	Sea Otters Captured males	Sea Otters Captured females	# of Foraging Dives Recorded	TDRs Analyzed
San Simeon (PBLA)	2.56**	<i>Stongylocentrotus franciscanus</i>	0.0004 (0.0008)	2001-2004	8	27	34,190	24
		<i>Stongylocentrotus purpuratus</i>	0.0048 (0.0131)					
		<i>Lithopoma gibberosum</i>	0.0057 (0.0094)					
		<i>Haliotis rufescens</i>	0.0006 (0.0009)					
San Nicolas Island (SNI)	0.33	<i>Stongylocentrotus franciscanus</i>	1.353 (1.4056)	2003	9	7	4734	4
		<i>Stongylocentrotus purpuratus</i>	11.460 (13.098)	2004	3	2		n/a
		<i>Lithopoma undosa</i>	0.1920 (0.4449)					
		<i>Haliotis rufescens</i>	0					
		<i>Haliotis corrugata</i>	0.0005 (0.0015)					
Post-translocation San Nicolas Island (old SNI)	uncertain	<i>Stongylocentrotus franciscanus</i>	2.699 (1.9043)	1988-1990	4*	8*	1209	n/a
		<i>Stongylocentrotus purpuratus</i>	28.236 (25.9793)					
		<i>Lithopoma undosa</i>	0.934 (0.7662)					
		<i>Haliotis rufescens</i>	0.071 (0.0645)					
		<i>Haliotis corrugata</i>	0.048 (0.0746)					

*otters for which > 50 known outcome foraging dives were recorded
 **Kage 2004

Table 3 Results of body metric comparisons of SNI and PBLA sea otters to age-adjusted measurements from below-equilibrium (1960s-70s) and at-equilibrium (1990s) Aleutian Islands populations. Statistics are the result of one-sample t-tests and standard deviations are shown in parentheses. Mean weights and lengths are adult averages.

Morphometry Comparisons	SNI		PBLA		
	Females	Males	Females	Males	
Mean Weight (kg)	24.47 (2.24)	35.26 (3.30)	18.69 (2.43)	25.94 (3.13)	
Mean Length (cm)	123.17 (3.71)	133.57 (2.83)	116.36 (3.92)	124.74 (3.89)	
Residuals from Aleutians Curves:					
1960s-70s weight	mean	2.62 (2.34)	7.46 (3.10)	-2.38 (-2.14)	-5.34 (-5.19)
	df	8	9	29	12.00
	t	2.89	7.6	-5.67	-0.54
	p	0.02	<0.001	<0.001	0.14
1960s-70s length	mean	17.40 (6.16)	27.71 (10.32)	8.76 (3.98)	14.10 (6.82)
	df	7	9	28	13.00
	t	7.99	8.49	11.84	7.74
	p	<0.001	<0.001	<0.001	<0.001
1990s weight	mean	-0.45 (2.27)	1.61 (4.51)	-5.35 (-5.19)	-5.24 (-5.21)
	df	8	9	29	12.00
	t	-0.60	1.13	12.75	-5.47
	p	0.57	0.29	<0.001	<0.001
1990s length	mean	3.10 (6.65)	8.96 (7.26)	-6.32 (3.94)	-3.03 (5.64)
	df	7	9	28	13.00
	t	1.32	3.9	-8.63	-2.01
	p	0.46	0.0008	<0.001	0.13

Table 4 Prey summary for three southern sea otter populations. Percentages are relative frequency of occurrence, with prey types common to all three populations in bold. Prey items that could not be identified to genus are placed into higher taxonomic groups. Prey items are further classified into 13 categories for analysis.

Common Name	Latin Name or Taxonomic group	Prey Category	% at SNI	% at 1988 SNI	% at PBLA*
red urchin	<i>Strongylocentrotus franciscanus</i>	urchin	46.88%	26.87%	0.02%
kelp crab	<i>Pugettia</i> spp.	kelp crab	21.65%	4.82%	20.05%
Cancer crab	<i>Cancer</i> spp.	cancer crab	7.26%	2.66%	10.43%
unidentified snail	various gastropod species*	snail	5.90%	1.14%	0
wavy turban	<i>Lithopoma undosa</i>	snail	5.77%	2.53%	0
purple urchin	<i>Strongylocentrotus purpuratus</i>	urchin	5.10%	18.38%	9.11%
unidentified crab	various decapod species	decapod	2.02%	3.04%	8.89%
unidentified urchin	<i>Strongylocentrotus</i> spp.	urchin	1.41%	3.80%	0
lobster	<i>Panulirus interruptus</i>	decapod	1.28%	1.39%	0
abalone sp.	<i>Haliotis</i> spp.	abalone	0.84%	6.84%	0.54%
octopus	<i>Octopus</i> spp.	cephalopod	0.70%	0.25%	0.36%
unidentified clam	various pelecypod species	clam	0.35%	0	14.25%
giant rock scallop	<i>Crassodoma multirugosus</i>	clam	0.13%	0	0.11%
chiton	<i>Mopalia</i> spp., <i>Tonicella</i> spp.	other (rock)	0	0	0.07%
fat innkeeper worm	<i>Urechis caupo</i>	worm	0	0	3.38%
gaper clam	<i>Tresus nuttalli</i>	clam	0	0	0.24%
isopod	various spp.	other (rock)	0	0	0.13%
limpet	<i>Diodora aspera</i>	other (rock)	0	0	0.01%
mussel	<i>Mytilus californianus</i>	mussel	0	0	8.51%
sand crab	<i>Emerita</i> spp, <i>Blepharipoda</i> spp.	other (sand)	0	16.22%	0.42%
sand dollar	<i>Dendraster excentricus</i>	other (sand)	0	0	0.91%
sea cucumber	various holothurian spp.	other (rock)	0	0.13%	0.09%
sea star	<i>Pisaster</i> spp.	sea star	0	0	3.24%
small kelp fauna	various small invertebrates	other (rock)	0	0	7.20%
squid	<i>Loligo</i> spp.	cephalopod	0	0	0.06%
turban snail	<i>Tegula</i> spp.	snail	0	0.00%	10.97%
unidentified worm	various annelid species	worm	0	0.00	0.21%
cockle	<i>Clinocardium nuttalli</i>	clam	0	0.00%	0.01%

*most likely small *Lithopoma*, *Tegula* spp., or *Norissia norissii*

Table 5 Bonferroni post-hoc pairwise comparisons for discriminant analysis Score 1 for all PBLA specialist types (1, 2, 3) and SNI.

Matrix of pairwise comparison probabilities:					
Type	SNI	1	2	3	
SNI	1.0000				
1	0.0015	1.0000			
2	<0.0001	0.0485	1.0000		
3	<0.0001	<0.0001	<0.0001	1.0000	

Table 6 Comparisons of the means and standard deviations in the estimated rate of energy gain for two populations. For each demographic group the standard deviation of the mean rate of energy gain represents within-individual (bout to bout) variation. Data are summarized for each study area, for females and (in the case of PBLA) for three foraging specialist types.

Study Area	Group	mean energy rate (kJ/min)	within individual σ	between individual σ
SNI	all animals	49.9	32.6	18.2
	reproductive females (n = 3):			
	with small pups	30.5	31.4	15.4
	with large pups	53.9	25.6	10.3
	no pups	54.1	24.7	9.1
PBLA	all animals	33.2	22.4	18.2
	type 1 females	43.8	30.1	21.1
	type 2 females	21.7	10.8	7.7
	type 3 females	28.2	14.5	6.5
	reproductive females			
	with small pups	*	*	*
	with large pups	45.3	26.66	37.54
no pups	38.8	30.26	17.99	

* data not available

Table 7 Comparison of telemetry (observational) and time-depth recorder (TDR) based feeding budgets for PBLA and SNI. For telemetry estimates n = number of otters; for TDR estimates n = number of days in the record. Means, standard error and confidence level for samples indicated by * are based on bootstrap resampling with 1000 iterations. For telemetry analyses, n = number of otters; for TDR analyses, n = number of days in record. TDR estimates for resting and other active for PBLA are still under analysis.

Study	Activity Category by Demographic Group	Telemetry Estimates				TDR Estimates					
		Mean %	std error	95% CL	n	Mean %	std error	95% CL	n (otters)	n (days)	
PBLA	Females	Feeding	43.34	0.24	0.47	47*	41.55	0.60	1.18	12	1764
		Resting	44.60	0.22	0.42		-	-	-		
		Other Active	11.50	0.08	0.16		-	-	-		
	Males	Feeding	35.46	3.49	7.48	15	43.86	0.64	1.25	9	53
		Resting	43.10	3.32	7.11		-	-	-		
		Other Active	21.50	2.56	5.48		-	-	-		
	All	Feeding	40.00	0.22	0.43	62*	39.78	2.21	4.63	21	2803
		Resting	43.70	0.18	0.36		-	-	-		
		Other Active	16.20	0.13	0.25		-	-	-		
SNI	Females	Feeding	22.73			6*	25.00	n/a	n/a	1	137
		Resting	57.00				70.00	n/a	n/a		
		Other Active	20.20				5.00	n/a	n/a		
	Males	Feeding	21.82	1.82	23.10	2	34.22	0.45	0.89	3	960
		Resting	48.00	8.00	10.26		55.64	0.53	1.05		
		Other Active	30.00	6.30	79.50		10.63	0.31	0.62		
	All	Feeding	22.60	0.10	0.20	8*	31.93	0.54	1.08	4	1097
		Resting	54.90	0.09	0.17		59.30	0.63	1.25		
		Other Active	22.6	0.11	0.22		9.16	0.31	0.62		
PCTN	Males	Feeding	n/a	n/a	n/a	38.32	0.67	1.3132	6	55	
		Feeding	n/a	n/a	n/a	36.7	3.21	6.35	10	1039	

Table 8 Foraging dive characteristics of SNI otters and 3 PBLA specialist types. Dive and surface intervals are in seconds. Prey size is relative to 5 cm increments (1 = 0-5 cm, 2 = 6-10 cm). Shown are means and standard deviations.

Characteristics	Foraging Type			
	SNI	Type 1	Type 2	Type 3
Prey Types	urchins and crabs	crabs and abalone	clams and worms	turban snails
mean % success	55.5 (7.6)	60.3 (12.2)	75.1 (7.7)	87.1 (1.9)
mean dive interval	39.3 (10.3)	61.4 (13.9)	61.5 (12.8)	71.6 (22.8)
mean surface interval	46.0 (18.6)	63.1 (23.1)	43.7 (11.8)	79.6 (10.8)
mean prey size	1.7	1.4	1	1

Figures

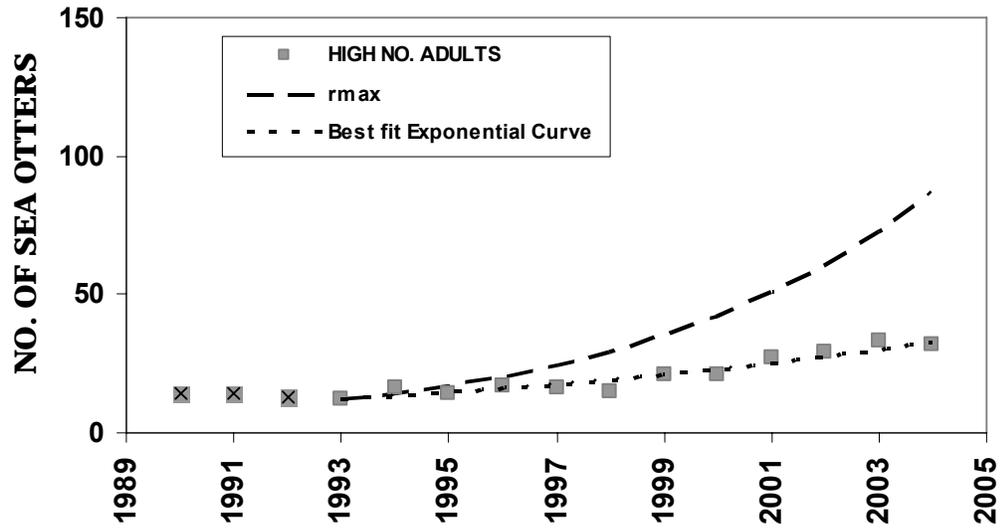


Figure 1 High counts of independent sea otters at San Nicolas Island based on U S Geological Survey quarterly censuses conducted following the translocation. r_{\max} is based on sea otter life history characteristics. Best fit exponential curve ($y = 6E-78e^{0.0904x}$) represents an 8.9% rate of growth since lowest count in 1993.

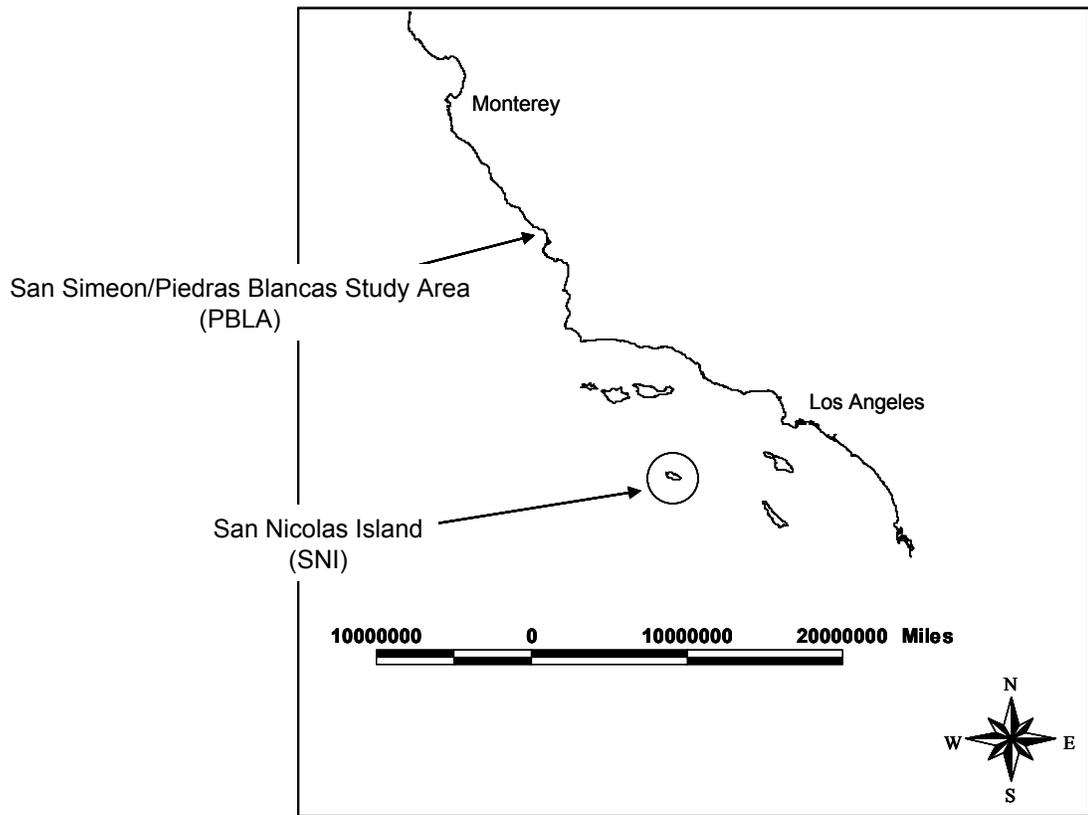


Figure 2 Map of California indicating the location of the two relevant study areas

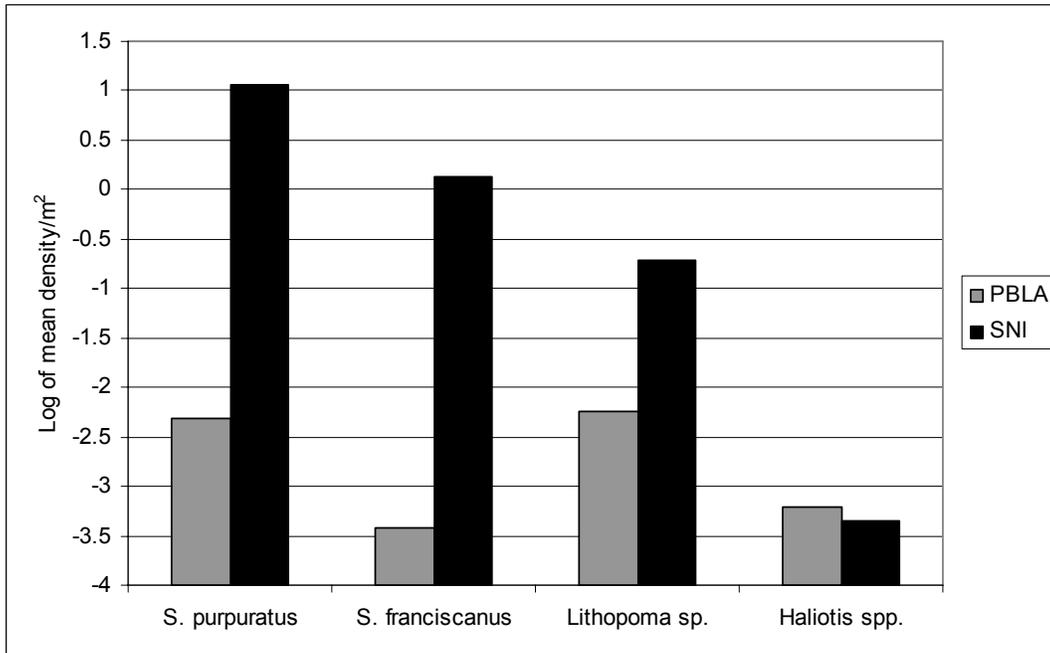


Figure 3 Densities of selected sea otter prey types for the two study areas. Note that data are log transformed. *Lithopoma* spp. are congeners *L. undosa* for SNI and *L. gibberosum* for PBLA. *Haliotis* spp. Are *H. rufescens* and *H. corrugata* for SNI (*H. rufescens* were present at negligible densities) and *H. rufescens* at PBLA.

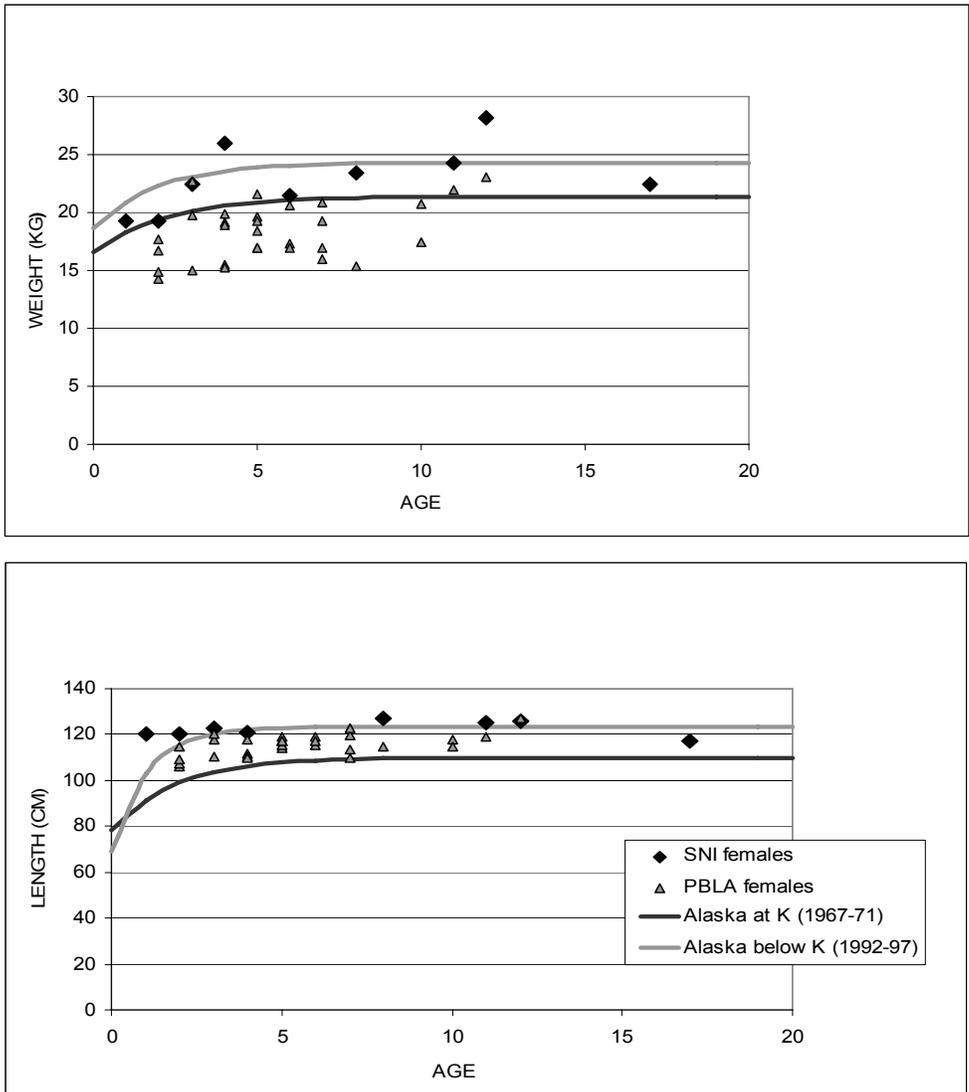


Figure 4 Plot of weight (kg) at age for females from SNI and PBLA in relation to growth curves from two Aleutian Islands populations at different stages of equilibrium density (K = carrying capacity).

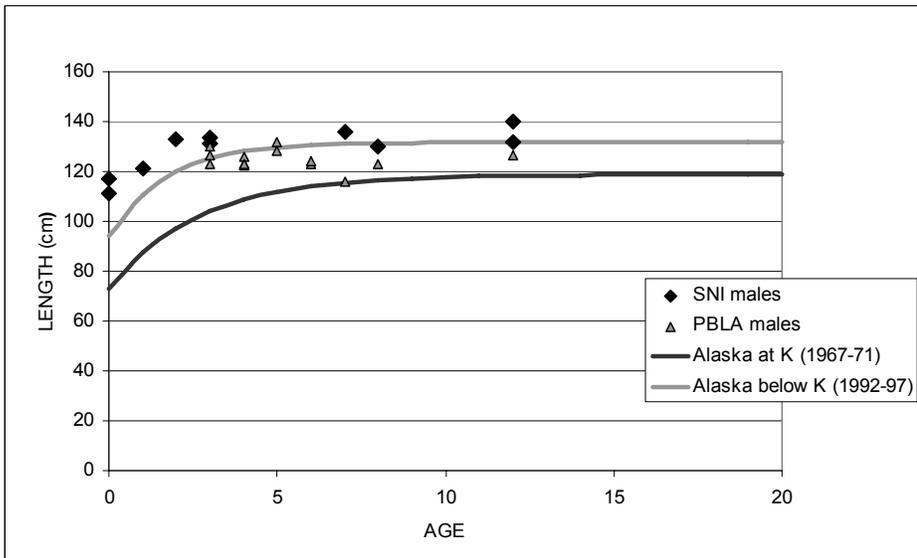
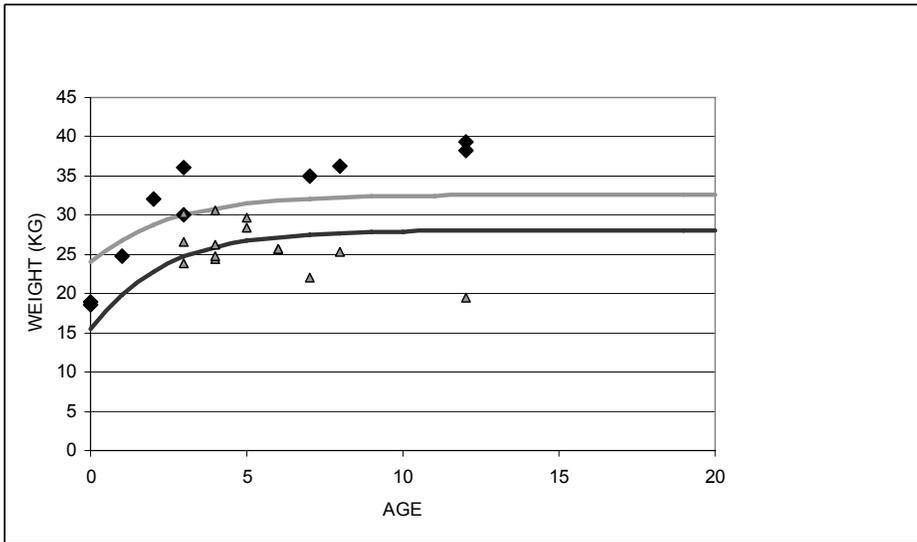


Figure 5 Plot of weight (kg) at age for males from SNI and PBLA in relation to growth curves from two Aleutian Islands populations at different stages of equilibrium density (K = carrying capacity).

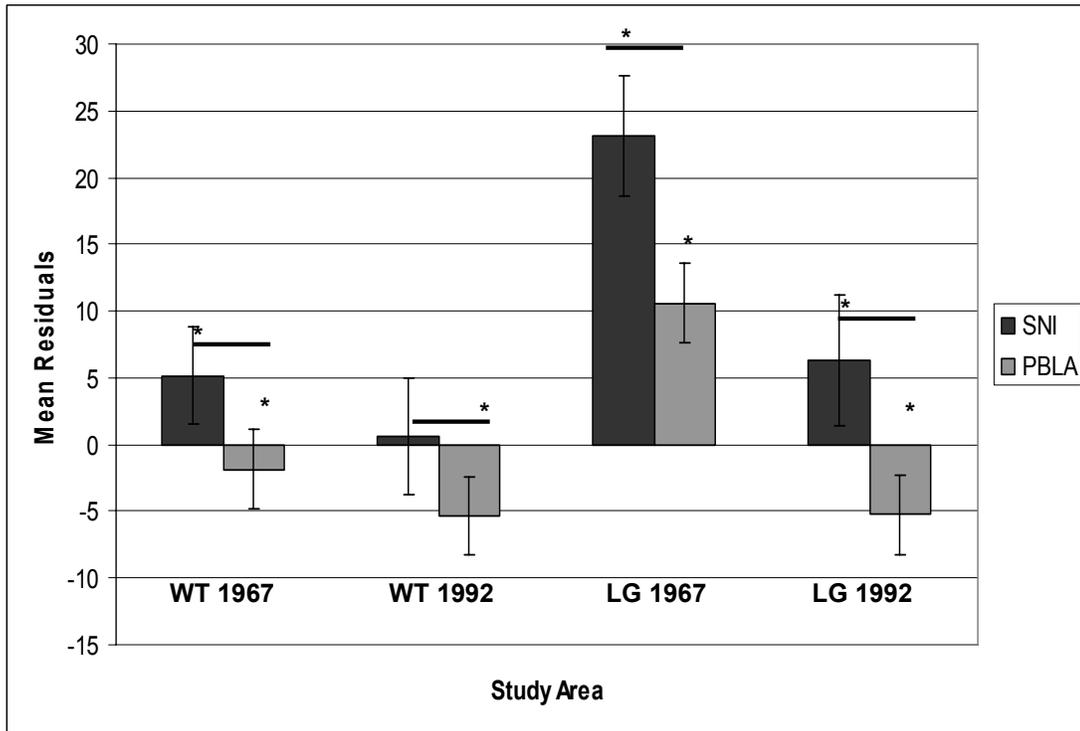


Figure 6 A comparison of residuals from two Aleutian Islands growth curves for mass (WT) and body length (LG) for SNI and PBLA. Asterisks denote values that are significantly different from the expected values (mean = 0). Floating bars denote residual values that differ significantly between populations. Error bars represent ± 1 standard deviation.

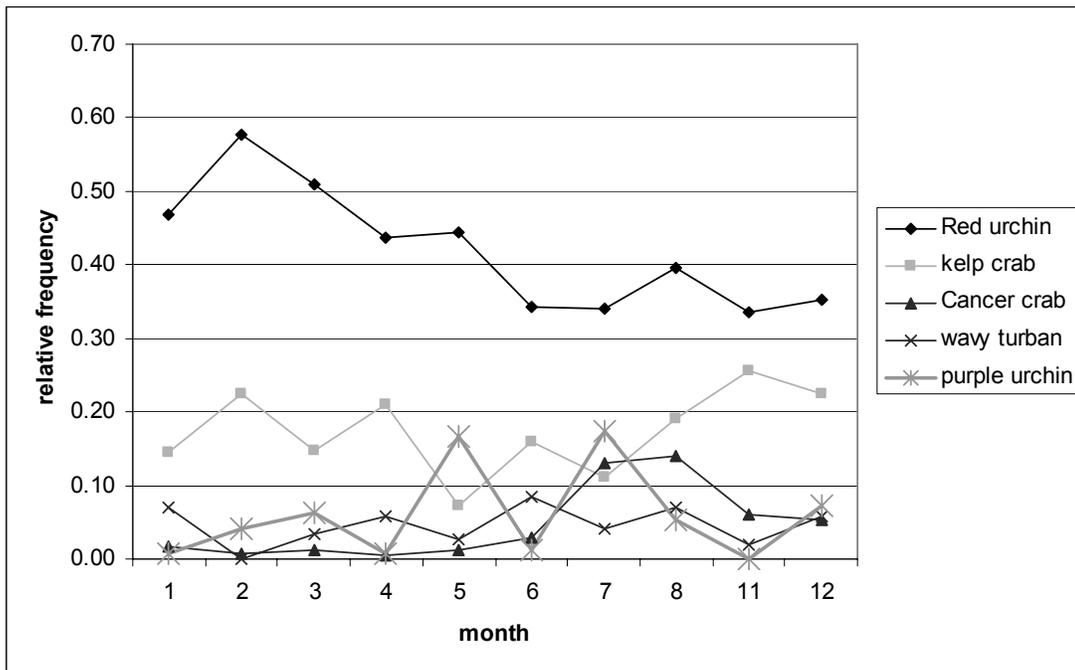


Figure 7 Relative proportions of five common prey types in the diets of sea otters at San Nicolas Island by month. Numbers on x-axis refer to months (January-December 2003). Data presented are limited to months in which >100 dives were recorded.

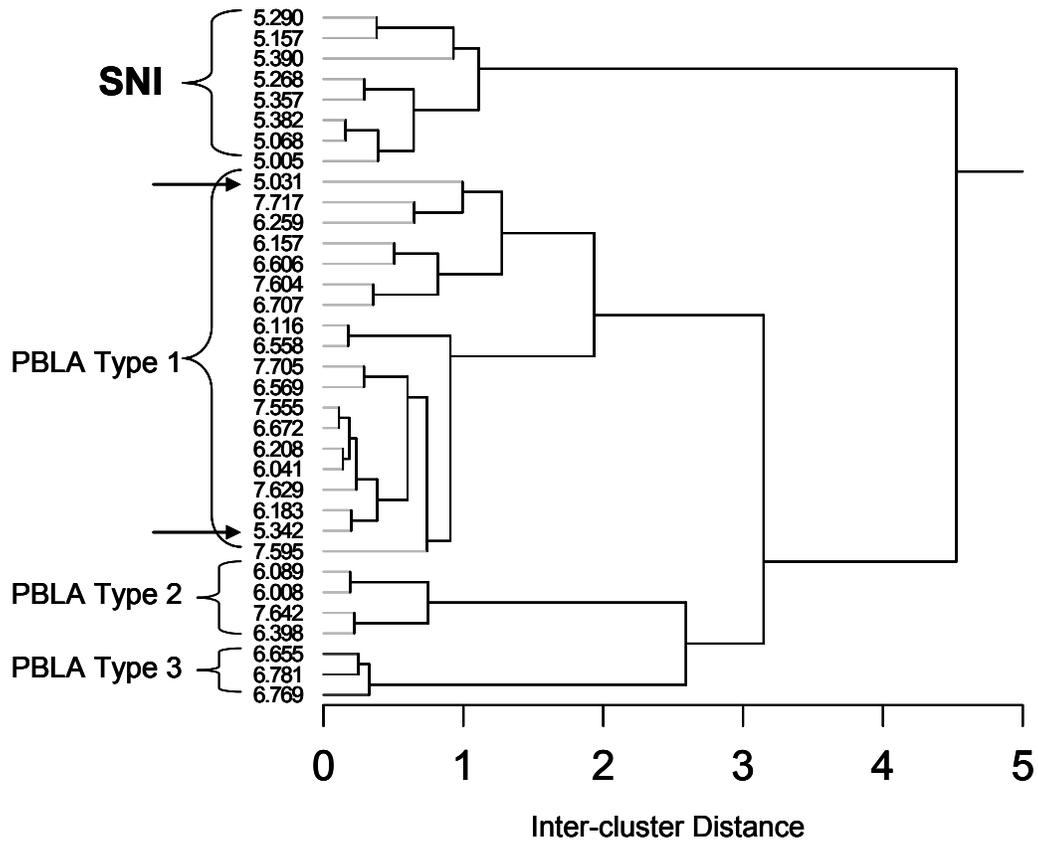


Figure 8 Dendrogram of the results of hierarchical cluster analysis based on the composition of 13 prey categories in the diets of individuals from SNI and PBLA. Types are designated based on cluster groupings and proportion of agreement with previous designations. Terminal nodes represent individual otters. SNI individuals that placed outside of the SNI group are indicated with arrows.

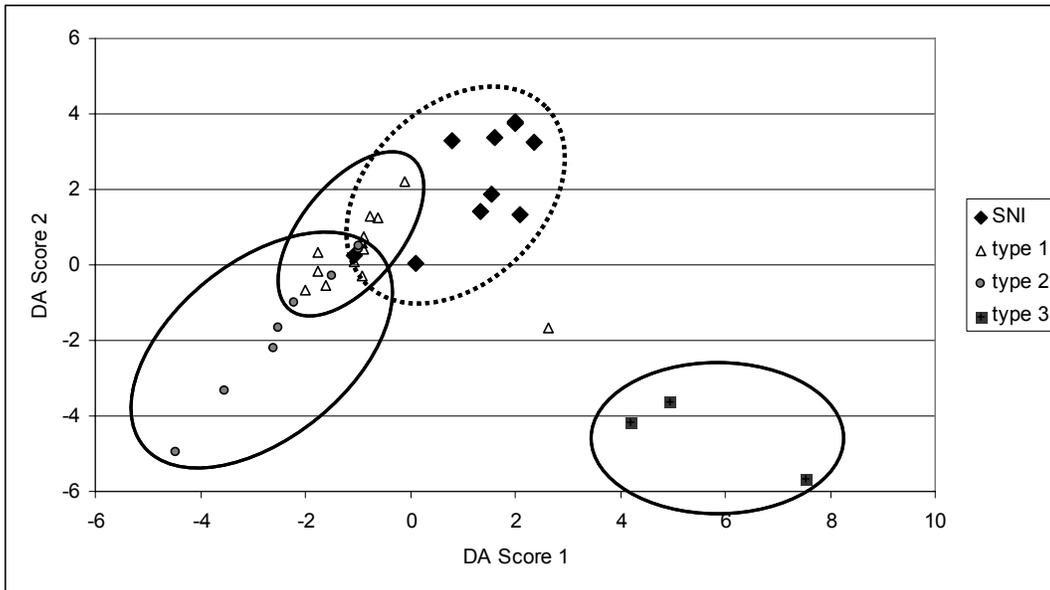


Figure 9 Plot of the first two discriminant analysis scores. Scores represent how prey types contribute to distinguishing groups designated by cluster analysis. Points are identified as individuals from SNI and three PBLA specialist types, with SNI indicated by dashed circle. See Appendix B for canonical discriminant functions.

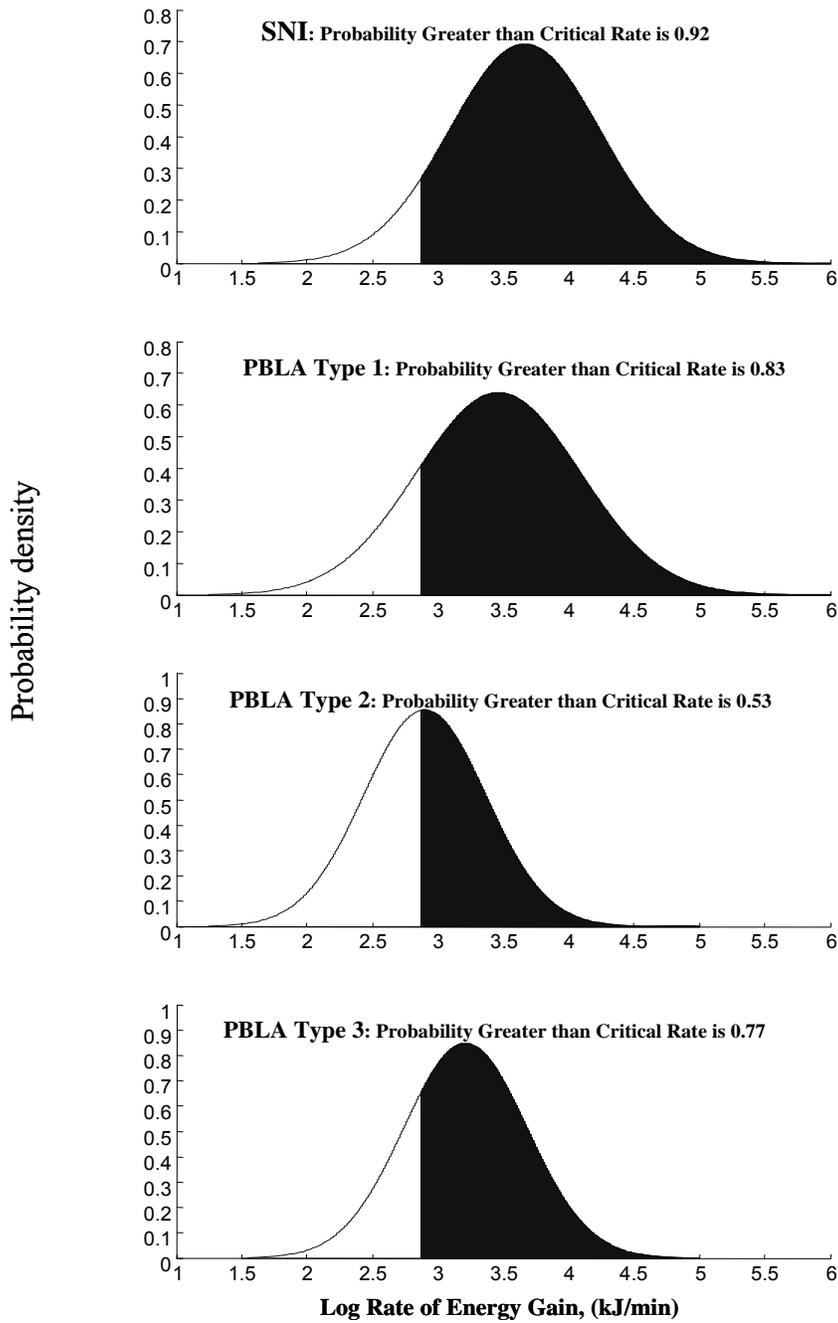


Figure 10 Density distributions of log transformed rates of energy gain (kJ/min) for females from SNI and the three PBLA specialist types. White segments of curves lie below an arbitrary “critical value” calculated as 90% of the average rate that would be required for an 18 kg female foraging for 65% of the day (based on published estimates of sea otter metabolic requirements).

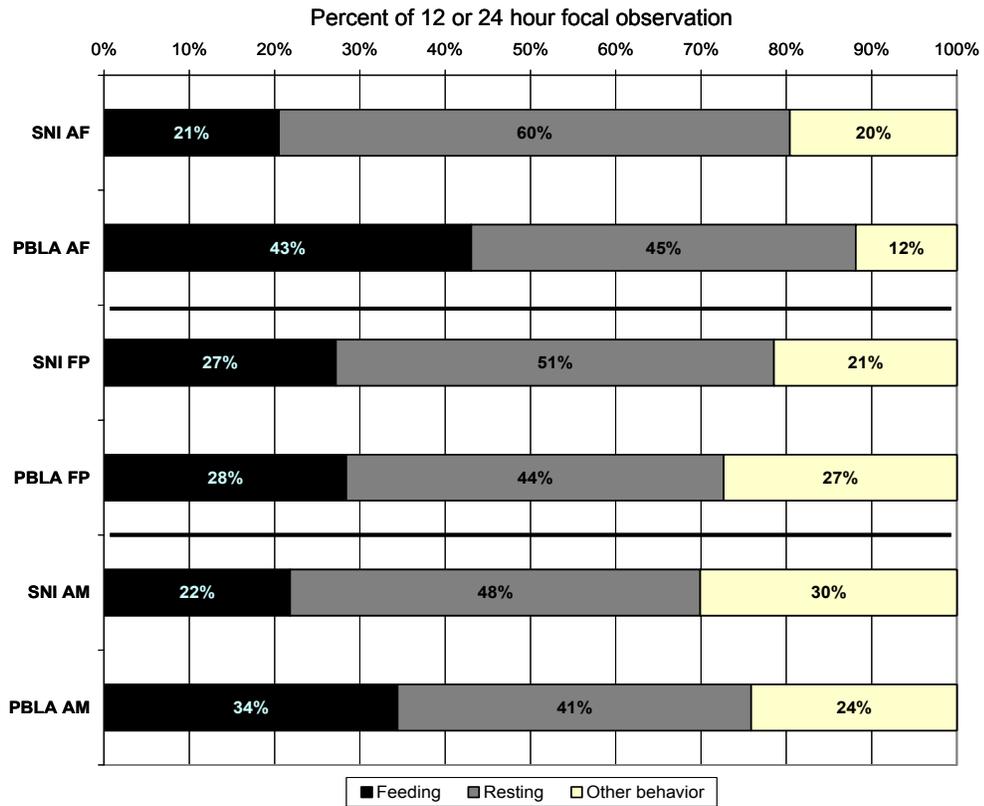


Figure 11 Comparisons of activity budgets between SNI and PBLA for three categories of activity. Other active includes all active behaviors other than feeding. Means are summarized for all sex classes and are based on 12 and 24 hour focal observations. A = adult, F = female, M = male, P = with pup.

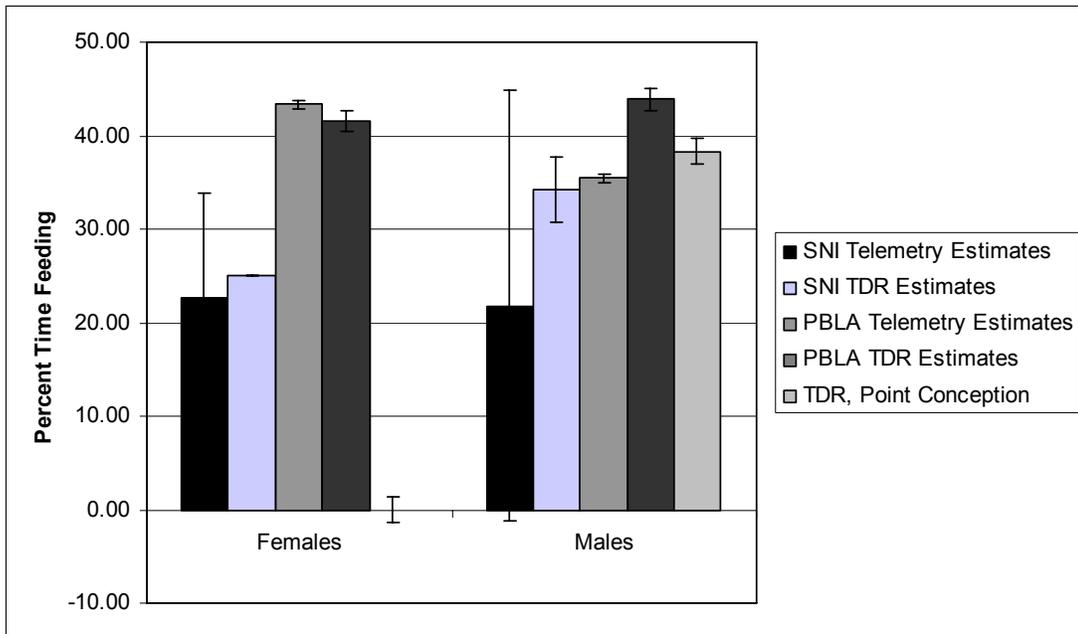


Figure 12 A comparison of telemetry and TDR-based estimates of feeding activity for SNI and PBLA. Data from Point Conception (PTCN) is included as a subset of the PBLA male sample. Error bars are 95% Confidence Interval.

Appendix A Parameters of von Bertalanffy growth curves (1 SE) fitted to mass (kg) and body length (cm) of male and female Aleutian Island sea otters from two populations of varying equilibrium density; 1967-1971 = at equilibrium, 1992-1997 = below equilibrium.(from Laidre et al., unpublished data)

		1967-1971			1992-1997		
Body Mass	A_{∞}	$k(\text{yr}^{-1})$	$t_0(\text{yr}^{-1})$	A_{∞}	$k(\text{yr}^{-1})$	$t_0(\text{yr}^{-1})$	
Male	28.1 (0.47)	0.44 (0.07)	-1.81 (0.66)	32.6 (0.47)	0.4 (0.07)	-3.33 (0.66)	
Female	21.4 (0.14)	0.44 (0.05)	-3.4 (0.71)	24.3 (0.47)	0.52 (0.07)	-2.79 (0.66)	
Body Length							
Male	118.7 (0.69)	0.38 (0.05)	-2.51 (0.64)	131.65 (0.47)	0.58 (0.07)	-2.17 (0.66)	
Female	110.03 (0.23)	0.53 (0.06)	-2.35 (0.52)	123.65 (0.47)	0.97 (0.07)	-0.85 (0.66)	

Appendix B Summary of Discriminant Analysis results. Within the table of discriminant functions, values shown in bold indicate the prey types that drove the formation of groups.

Prey Type	F-to-Remove	Standardized Canonical Discriminant Functions			
		Factor 1	Factor 2	Factor 3	Total (absolute)
abalone	1.140	0.141	0.025	0.597	0.763
bivalve	13.740	-0.410	-0.629	0.928	-0.110
Cancer crab	2.800	-0.213	-0.130	-0.829	-1.172
cephalopod	0.510	0.079	0.057	-0.355	-0.218
crab (un-id)	2.560	-0.355	-0.248	-0.562	-1.165
kelp crab	0.360	0.104	0.240	0.191	0.535
other (rock)	1.190	0.161	0.350	-0.866	-0.355
snail	15.500	0.825	-0.558	0.025	0.292
sea star	0.090	0.059	-0.066	0.136	0.129
urchin	8.100	0.469	0.703	0.769	1.941
mussel	0.480	-0.083	-0.235	-0.209	-0.527
other (sand)	1.340	-0.216	-0.429	0.870	0.224

Group Means	Cluster 1	Cluster 2	Cluster 3	Cluster 4
abalone	0.432	1.615	0.261	0.518
bivalve	0.000	1.283	10.009	0.767
Cancer crab	2.043	15.560	7.321	1.525
cephalopod	0.321	0.379	1.065	0.095
crab (un-id)	0.322	1.615	0.679	0.385
kelp crab	1.703	1.910	0.950	0.902
other (rock)	0.012	0.272	0.283	0.007
snail	1.243	0.470	0.003	10.125
sea star	0.000	0.551	0.411	0.761
urchin	6.059	1.432	0.662	0.061
mussel	0.000	1.645	0.056	0.057
other (sand)	0.000	0.016	0.032	0.000

Diagnostic Statistics

Wilks' lambda= 0.0048
 Approx.F= 7.9308 df = 36 56 prob = 0.0000

Pillai's trace= 2.489
 Approx.F= 8.524 df= 36, 63 p-tail= 0.0000

Lawley-Hotelling trace 14.983
 Approx.F= 7.353 df= 36, 53 p-tail= 0.0000

Appendix B, cont'd

Group Frequencies:	Cluster 1	Cluster 2	Cluster 3	Cluster 4
	8	19	4	3

Classification matrix (cases in row categories classified into columns)

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	% Correct
1	8	0	0	0	100
2	1	18	0	0	95
3	0	0	4	0	100
4	0	0	0	3	100
Total	9	18	4	3	97

Jackknifed classification matrix

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	% Correct
1	8	0	0	0	100
2	1	16	1	1	84
3	0	1	3	0	75
4	0	0	0	3	100
Total	9	18	4	3	88

Factor Eigenvalues:	5.8352141	5.2817899	3.8658886
Canonical correlations:	0.9239582	0.9169568	0.8913404
Cumulative proportion of total dispersion:	0.3894584	0.7419798	1.0000000

Appendix C Energy content by size class for invertebrate prey items from SNI and PBLA diets. Values are derived from published literature as compiled in Tinker (2004). Prey items represented in both SNI and PBLA diets are shown in bold.

Prey Type	Mean Size Class		Energy Content (kJ per prey item)			
	SNI Diet	PBLA Diet	size 1 (1-5 cm)	size 2 (6-10 cm)	size 3 (11-15 cm)	size 4 (>15 cm)
red urchin	2	1	14.7	142.8	571.5	-
kelp crab	1	1	19.9	40.4	65.4	-
Cancer crab	3	2	47.8	261.3	1428.1	2183.9
unidentified snail	1	1	3.0	25.3	-	-
wavy turban	2	-	29.0	67.0	-	-
purple urchin	1	1	5.6	104.6	-	-
unidentified crab	2	1	33.8	150.8	1307.6	-
unidentified urchin	1	-	5.6	104.6	-	-
lobster	4	-	31.0	261.3	1428.1	2183.9
abalone sp.	4	3	28.3	229.9	704.2	3637.8
octopus	2	2	15.0	208.6	870.8	-
unidentified clam	1	1	8.6	99.1	394.0	-
giant rock scallop	2	3	8.0	85.1	-	-
chiton	-	1	6.7	49.8	-	-
fat innkeeper worm	-	2	25.5	51.4	51.4	-
gaper clam	-	2	9.1	107.3	382.8	-
isopod	-	1	10.0	-	-	-
limpet	-	1	6.7	49.8	-	-
mussel	-	1	2.5	37.4	-	-
sand crab	-	1	10.0	-	-	-
sand dollar	-	1	5.0	-	-	-
sea cucumber	-	1	7.5	20.0	25.0	-
sea star	-	2	5.5	35.8	42.6	-
small kelp fauna	-	1	10.0	-	-	-
squid	-	1	6.8	104.3	435.4	-
turban snail	-	1	25.3	-	-	-
unidentified worm	-	2	12.7	25.7	25.7	-
cockle	-	1	8.1	97.2	247.7	-

