# Biological Analysis of Sea Otters and Coastal Marine Ecosystems in Central and Southern California: Synopsis and Update

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In the late 1980s and early 1990s, 140 sea otters were translocated from central California to San Nicolas Island in an effort to enhance recovery of this legally threatened population. Formal authority to conduct this translocation included the requirement that a management zone be designated, in part to reduce potential conflicts between sea otters and shellfisheries interests in southern California. As a consequence, the remaining coastal waters of southern California were designated a "management" or a "no-otter" zone. Any sea otters entering this zone, either from San Nicolas Island or central California, were to be captured and removed. In the years that have ensued since the translocation, the relocated colony at San Nicolas Island has not grown as hoped and expected, and the sea otter population in central California has expanded its range southward with occasional large numbers of sea otters moving beyond Pt. Conception into the no-otter zone. The US Fish and Wildlife Service (FWS) is presently considering how to deal with these issues and problems. A number of management options have been envisioned. These are articulated and discussed in the FWS Draft Supplemental Environmental Impact Statement: Translocation of Southern Sea Otters, and a preferred alternative has been identified (although not formally selected).

Regardless of the final decision, the process of selecting a management option by FWS likely will result in significant discussion and controversy. These discussions and debates will require scientific information that is as accurate, complete and up-to-date as possible. Much of the relevant information is available in the peer-reviewed scientific literature, in various other reports and documents, and on publicly accessible websites maintained by the US Geological Survey, the Fish and Wildlife Service, and the California Department of Fish and Game. However, because of the ever-changing and dynamic nature of both the analysis of this information and the status of the sea otter populations, such sources can quickly become dated and even incorrect. The purpose of this white paper is to provide a synopsis and update of relevant biological information on sea otters and their coastal ecosystems. This document is not intended to support any particular management decision or policy agenda; it is simply an effort to provide accurate and up-to-date information for those involved in these discussions and debates.

#### Population trends—Central California

Trends in the distribution and abundance of sea otters in central California are assessed using range-wide, uncorrected counts of the entire population that are conducted twice annually--in late spring and early autumn. The late spring counts are considered to be the more reliable of the two data sets and are thus used as the primary indicator of change in population distribution and abundance. Because these data represent minimum population counts, with no associated correction factor or variance estimate, they include a significant (but unmeasurable) sampling error component, reflecting year-to-year variance in survey conditions and viewing conditions. Accordingly, in order to reduce potential influences from the vagaries of any single census, these data are plotted as 3-year running averages, and the trends in these averages are used by FWS to assess longer-

term population trends. These data are available at (<a href="http://www.werc.usgs.gov/otters/casurvey3yr.html">http://www.werc.usgs.gov/otters/casurvey3yr.html</a>).

In addition to the annual population counts, a number of other independent sources of data (discussed below) allow for assessment of the underlying demographic shifts that drive population change. Of the 3 main factors that can result in variation in abundance (reproduction, mortality, and movement), variation in mortality has been found to be the principal driver of the patterns and trends of population growth in the California sea otter, while birth rates have remained more or less constant. Many of the deaths appear as stranded carcasses, and thus the stranding record is of considerable interest in understanding the dynamics of the living population. Beached carcasses are obtained opportunistically, usually from reports by others. A variety of standardized measures are recorded for each carcass, including date, location, age (from tooth sections), sex (when possible), condition, and cause of death (when possible). Fresh carcasses are necropsied by trained veterinary pathologists with the California Department of Fish and Game.

Although the currently-used method of population assessment was initiated in 1982, information on the abundance and distribution of California sea otters is available from a variety of sources and methods since the early 20<sup>th</sup> century (Riedman and Estes 1990). These collective data indicate a slow but consistent rate of increase at about 4-5% yr<sup>-1</sup> through the mid 1970s. Then, in about 1975, the population began a period of marked decline, which continued through the early 1980s. In 1983 it was discovered that California sea otters were being entangled and killed in a coastal set net fishery, and prohibitions were put in place to reduce or eliminate these losses. Immediately thereafter the population resumed its earlier rate of increase. Population growth continued until about 1995, at which point the numbers again began to decline. This latter decline continued through the 1990s and then stabilized, and since 2003 the counts have increased.

The most recent trend of population increase appears to have been driven largely by increases in some component of the population other than reproductive females, probably males but possibly also including non-reproductive (sub-adult) females. This conclusion is based on two findings: 1) the number of females with dependent pups counted during the survey (presumably an indicator of reproductive female abundance, if we assume constant birth rates) has not increased, and in fact has not changed appreciably since the early 1990s; and 2) the count increases have occurred in areas of the range that are known or suspected to be inhabited primarily by males and juvenile females. Reasons for these recent population trends and apparent shifts in sex ratio are uncertain; however, what is certain is that the increasing trend will not be sustainable unless the number of reproductive females also increases, as it is this component of the population that ultimately determines long-term population growth.

A detailed analysis of the stranded carcass records through 1999 is provided by Estes et al. (2003). Several interesting patterns are evident in these analyses. The death assemblage contains a large number of prime age (4-9 year old) females. This is important because prime age females are the principal demographic drivers of population

growth and surprising because mortality rates in this segment of sea otter populations elsewhere are normally quite low (except for instances where exogenous sources of mortality, such as oil from the Exxon Valdez spill in Prince William Sound or predation by killer whales in southwest Alaska, indiscriminately kill sea otters of all age and sex classes). A second important pattern from the death assemblage analysis is the existence of frequent strandings throughout the year, with a higher level of carcass recoveries from late spring to late summer. This finding was also unexpected, as strandings elsewhere tend to be highly seasonal events, normally occurring in late winter/early spring. A third intriguing pattern in the death assemblage analysis is that per capita mortality rate (measured as the number of carcasses retrieved during the calendar year divided by the number of otters counted during the spring surveys in that same year) was correlated with population trend, being relatively higher during periods of sustained population decline. These patterns, together with the number of deaths attributed to attacks by great white sharks, were more pronounced during periods of population decline than during periods of population increase. Although infectious disease was the leading overall cause of death, this pattern did not vary between periods of population increase and decline. Per capita pup production and body condition (as measured by mass/length ratios of adult carcasses) both declined over the 31 year period of the study, although it appears that the gradual decrease in per capita pup counts reflects a shift in the age-sex composition of the population (i.e. relatively more males and juveniles), possibly in conjunction with increased pre-weaning mortality, and not a decrease in age-specific birth rates (Tinker et al, in press). While a similarly detailed analyses of the most recent data are not currently available, the per capita mortality rate appears to have increased since about the early to mid 1990s. Most notably, there has not been a concurrent decline in this measure of per capita mortality in association with the most recent increases in population counts.

#### Population trends—San Nicolas Island

By 1990, most of the 140 sea otters that were translocated to San Nicolas had disappeared from the island. All of the translocated animals were tagged for individual identification prior to release, and the fates of about half of these are known. Many of the missing animals returned to almost their exact points of capture in central California. Dispersal away from San Nicolas Island rather than on-site mortality is thus thought to be the primary reason for the sharp post-release population decline. However, the proportion of missing animals that survived can not be determined, as many of them were never again seen. Forty-nine (35%) of the individuals that went missing from San Nicolas Island were later seen alive along the southern or central California mainland or on San Miguel Island. This value represents a minimal survival estimate for those animals that went missing from San Nicolas Island following the translocation.

The number of sea otters counted at San Nicolas Island remained roughly constant from 1990 through 1998, fluctuating between 15 and 19 (independents plus dependent pups; the number of independent animals over this same time period fluctuated between 12 and 17). In 1999, the counts began to increase, reaching a high of 38 (total) in 2003 (Hatfield 2005). Although this increment seems relatively modest in terms of absolute numbers, it nonetheless represents a period of exponential population increase at approximately 10%

per year, a rate that exceeds the maximum growth rate of the mainland population. However the counts at San Nicolas Island have since declined—to 35 in 2004 and 32 in 2005. Reasons for these recent patterns of population change at San Nicolas Island presently are not understood. Although the increasing counts from 1999 through 2003 almost certainly reflects intrinsic population growth, the question of whether the lower counts in 2004 and 2005 represent a cessation of population growth (and possible decline) or vagaries from the survey methodology is less clear. However, the fact that the counts have now declined in two successive years, after having increased over each of the preceding 5 years, suggests that the sea ofter population at San Nicolas Island is no longer increasing and may be in decline.

Overall, reproductive output by sea otters at San Nicolas Island appears normal (i.e. within the range reported for virtually all other sea otter populations). A minimum of 97 pups have been born at San Nicolas Island since 1990. There are no apparent trends in reproduction through time, with the minimum number of births ranging between 4 and 8 per year. Given the normal maximum longevity of wild sea otters (15-20 years) and the fact that at least one of the original animals translocated to San Nicolas Island was still alive in 2004, the observed birth rate is sufficient to have driven a much higher rate of population increase. These findings are consistent with the conclusion that failure of the San Nicolas population to increase more rapidly is the result of elevated mortality and/or dispersal away from the island. While the possibility of dispersal in recent years should not be completely discounted, there is no evidence for dispersal by any of the animals captured in 2003 and 2004 that were fitted with transmitters. Another factor that may also be significant at small population sizes is demographic stochasticity: in particular, it is conceivable that (by chance alone) the sex ratio of pups born at the Island might have varied significantly from 1:1, resulting in a skewed sex ratio. If this were the case, the number of females reaching reproductive age may have tapered off over recent years, in which case we would expect to see a leveling-off (or even a decrease) in the number of pups born at the Island. Unfortunately, it is often difficult or impossible to distinguish between alternative demographic explanations based on count data alone.

## Further insights into the demography of California sea otters

There are three kinds of available data on California sea otters that can be used to infer the demographic processes underlying the dynamics of the population. These are the time series of population counts (discussed above), data from the stranded carcasses (also discussed above), and information from marked animals in the living population. Several recent analyses have utilized this information in an effort to better understand the population dynamics of California sea otters. Not surprisingly, an analysis based on the proximate causes of mortality as determined from the stranded carcasses showed that future population growth was most sensitive to the rate of mortality from infectious disease (Gerber et al. 2004). A great deal has been learned in recent years about the proximate causes, vectors and spatial distributions of particular infectious diseases affecting sea otters in California, such as protozoal encephalitis, acanthocephalan peritonitis, myocarditis and cardiomyopathy (Kreuder et al. 2003, Kreuder et al. 2005, Mayer et al. 2003, Miller et al. 2002, Miller et al. 2004). However, while these diseases

appear to represent the primary cause of death in a majority of the fresh carcasses analyzed, it is less clear whether or not there is any common underlying or ultimate explanation for this pattern (e.g. elevated terrestrially vectored pathogen loads, density-dependent nutritional limitation, immune suppression due to low genetic diversity or contaminant burdens). Moreover, all conclusions about the impact of specific diseases on the population are founded on the crucial assumption that distribution of causes of mortality in carcasses for which cause of death is determinable (those that are reasonably fresh) is representative of mortality in the entire population. Violations of this assumption would occur if either the older and more deteriorated beach-cast carcasses are subject to a different overall mortality distribution or if the carcasses that strand have a different death structure from those that do not strand. These assumptions and alternative possibilities have not yet been rigorously evaluated.

A more recent and comprehensive analysis of demographic trends that utilized all three data types (carcass data, population counts and radio telemetry data from tagged animals) has resulted in two important conclusions (Tinker 2004 and Tinker et al. in press). One is that mortality rates vary substantially across the sea otter's range: in particular, juvenile and sub-adult mortality is higher in the northern half of the range (i.e. near the Monterey Peninsula) than in the central portion of the range (near Cambria), while mortality of all age classes is lowest at the southern end of the range (near Pt. Conception). The other is that mortality rates have increased significantly over the past 20 years, with a fairly substantial jump in the death rate occurring around 1995 and persisting through to at least 2003. This increase in mortality was most pronounced among prime-age and older females in the north and center of the range: in contrast, male mortality rates appear to have actually dropped somewhat since the mid 1980s, based on a comparative analysis of telemetry data from the two periods. Thus while the census data show an overall increase in abundance since 2001, these more detailed analyses indicate that the welfare of adult females, particularly in the north and center of the range, remains poor. This apparent discrepancy can be reconciled if the recent population increases are comprised disproportionately of males, as appears to be the case. Further data collection and analyses will be required to determine when and if adult female survival improves, as will be required for sustained population recovery, and to better understand the causes of spatial and temporal variation in mortality. Clearly infectious disease is foremost among the proximate drivers of this variation, but the more difficult challenge of understanding the ultimate explanation for high levels of disease is just beginning.

## Range expansion of California sea otters

One of the most important questions about the conservation of California sea otters concerns the degree to which the population's abundance and range will change in the years to come. Any such predictions are of course problematic because it is impossible to know how the various factors that influence reproduction, survival, and redistribution will change in the future. Nonetheless, the range of the California sea otter has been slowly but continuously increasing (especially to the south) and methods are now available wherein spatially explicit information on demography and individual movements can be used to forecast range spreading. It is further possible to evaluate the

sensitivity of these forecasting exercises to changes in critical demographic factors, such as age and sex-specific mortality and dispersal.

Such a forecasting analysis has been conducted for the spread of sea otters into southern California over two future time periods—10 and 25 years (Tinker et al. in review). The analytical approach was "ground truthed" by applying the algorithm to observed range expansion in past years, and was found to provide a good fit. Assuming no substantial change in the demography or behavior of sea otters, these analyses indicate that in 10 more years sea otters will have spread southeastward to about Santa Barbara (with a total of 65 individuals occurring south of Pt Conception), and in 25 years from present the range will have spread to about Carpinteria (with a total of 185 individuals occurring south of Pt. Conception). Perhaps more interesting than the point estimates themselves was the substantial degree of uncertainty associated with the predictions: for example, the 95% confidence interval around the estimated number of animals south of Pt. Conception after 25 years was 60 - 361 individuals. This uncertainty was mostly attributable to variation in the estimated survival rates of prime-age females, and to a lesser degree the movement rates of sub-adult females. Improved precision of the model predictions can thus be achieved by improving our estimates of these two parameters. More importantly, if the recent decline in female survival (particularly in the center of the range) is density dependent, as appears to be the case (see below), then recovery and delisting of the southern sea otter will depend on population growth near the ends of the current range, as well as range expansion into southern California (Tinker et al. in review).

#### Population status of sea otters in California

Further assessment of the population status of sea otters in central California can be achieved through the comparison of information between central California and San Nicolas Island. This assessment is based on contrasts in food availability, and the body condition and foraging behavior of sea otters, between these sites. Because of the small number of otters at San Nicolas Island and their recent occupation of that environment, food availability was assumed not to be the essential limiting resource for that population. The overall density of benthic invertebrate prey was indeed much greater (1-2 orders of magnitude) at San Nicolas Island than in central California (Bentall 2005), thus supporting this view. Furthermore, the length and mass at age, and the age-specific mass to length ratios were significantly greater for sea otters at San Nicolas Island than in central California. Finally, both dietary composition and time spent foraging varied in predictable and consistent ways between these two populations. The diets of sea otters at San Nicolas Island were diverse at the level of individuals, relatively narrow at the population level, and similar across different individual otters. The dietary patterns of sea otters in central California were quite different, being comparatively narrow at the level of individuals, diverse at the population level, and divergent across different individual otters. Time spent foraging and foraging bout lengths for otters were also much less at San Nicolas than in central California. These collective patterns indicate that food limitation is acting far more strongly on sea otters in central California than at San Nicolas Island, thus suggesting that sea otters in central California may be at or near the environmental carrying capacity. These findings have important implications for

conservation and management because they strongly suggest that future population growth (and thus delisting) of California sea otters will most readily be achieved through range expansion rather than increased population density within the present range.

#### Fate of translocated animals

Because the relocation of sea otters is part of several of the management scenarios being considered by FWS, it is important to review what is currently known or thought about the fate and behavior of sea otters that are captured and released elsewhere. Both the results of the translocation to San Nicolas Island and other shorter-distance relocations within the sea otter's range in central California indicate that individuals of this species have a strong affinity for their established home range, thus displaying the strong tendency to return to these sites when moved elsewhere. This means that many of the animals that might be moved to central California from either San Nicolas Island or elsewhere in southern California will probably attempt to return to their capture locations. The relocation of sea otters also involved an increased risk of mortality. This is due in part to the stress associated with capture, handling, and time out of the water. It may also result from the general lack of familiarity by the animals with their new environments. For males there is the added risk of death or injury from encountering territorial males in these foreign habitats. A third issue of concern is the possibility of detrimental effects of the foreign, relocated animals on the recipient population. Although such effects are as yet undocumented, they are especially likely when food resource competition is intense, as seems to be the case in the center of the current mainland range.

#### Ecosystem effects of sea otters in southern California

Like many other apex predators (Ray et al. 2005; Pace et al. 1999; Schmitz et al. 2000; Soulé et al. 2002; Soulé and Terborgh 1999; Terborgh et al. 2001; Hebblewhite et al. 2005), sea otters strongly impact the structure and function of their associated ecosystems. These ecosystem-level effects result in one way or another from the demographic or behavioral influences of the predators on their prey (i.e., what ecologists refer to as "direct effects"). Sea otters feed on a wide array of benthic invertebrate species, including but not limited to sea urchins, crabs, clams, mussels, abalones, and other gastropod mollusks. Populations of many of these prey species must have increased markedly after sea otters were removed from the North Pacific Ocean's coastal ecosystems during the maritime fur trade, or perhaps even earlier if aboriginal hunters also limited sea otters. Similarly dramatic prey population declines have occurred as the remnant sea otter colonies that survived the fur trade recovered and spread back into parts of their historical range. These effects have been documented at a number of locations, from the western Aleutian Islands to central California.

## Direct Effects

Because many of the sea otter's prey species are also valued as food by humans, commercial and recreational shellfisheries developed following the population increases of these prey species that occurred in the sea otter's absence. Not surprisingly, the

recovery and range-spread of sea otter populations into areas now utilized by shellfishers have produced conflicts and disagreements. The sea otter's proponents have argued that shellfish stocks have been exploited at unsustainably high rates, and thus that sea otters are not solely responsible for the decline or collapse of shellfisheries. This claim is true in some instances, the southern California abalone fishery being a case in point. In contrast, the proponents of shellfisheries have argued that sea otters were a primary cause of the collapse of certain fisheries, and that shellfisheries and sea otters cannot coexist (or more specifically, that although the shellfish populations themselves persist in the presence of sea otters, they do so at densities too low to sustain a profitable fishery). This claim is also true in many instances. The question of whether or not specific shellfisheries are economically sustainable in the absence of sea otter predation is beyond the scope of this summary. However, unsustainable shellfisheries are clearly evident from the present historical record, and sea otter predation clearly has caused or contributed to the collapse of a number of these shellfisheries. It is at least reasonable to conclude that sea otters cannot coexist in the same areas with many commercial shellfisheries. This is probably true for all shallow water dive-based fisheries for sea urchins and mollusks.

White abalones, which historically ranged from southern California to at least central Baja California, are now highly endangered and thus the reestablishment of sea otters could act to the detriment of the survival of this species. Sea otters and white abalones apparently coexisted during historical and prehistorical times, and the recent demise of white abalones clearly was caused by some factor or factors other than sea otter predation.

#### Indirect Effects

The ecosystem-level influences of predators are not limited to direct effects on their prey populations. Direct effects often lead to what ecologists term "indirect effects". The indirect effects of predation are more complex, more difficult to study, and thus much more poorly known and understood than are the direct effects. However, a large body of accumulating findings from many different predator species and their ecosystems is showing that the indirect effects of predators are often dramatic and wide-ranging across species and ecosystem processes. These indirect effects have been extensively studied and are comparatively well known for sea otter-kelp forest ecosystems (Estes et al. 2004, Estes 2005).

The most well known and extensively studied indirect interaction resulting from sea otter predation is the 3-trophic level interaction that occurs among sea otters, sea urchins, and the kelps and other fleshy macroalgae (creating what has been referred to as a "trophic cascade" [Paine 1980, Carpenter and Kitchell 1993]). In the case of sea otters and kelp forests, sea otters eat sea urchins and sea urchins eat kelp. Thus, where sea otters are present in sufficient numbers, sea urchins are rare (because the otters have eaten them) and kelp forests flourish (because the sea urchins are rare). In contrast, systems lacking sea otters are characterized by more abundant sea urchins and extensively overgrazed kelp forests. These overgrazed habitats have been termed "sea urchin barrens" because of the lack or near absence of kelps and other fleshy macroalgae.

The trophic cascade among sea otters, sea urchins, and kelps further influences the ecosystem in three general ways—by altering primary production (the highly productive kelps fix large quantities of inorganic carbon through photosynthesis), by creating threedimensional habitat for other species (much as terrestrial forests create habitat for insects, birds, and numerous other species), and by reducing the force of coastal waves and currents (in an analogous manner to the way that wind velocity is attenuated by terrestrial forests). These general processes have far-ranging effects on other coastal marine species. For example, the growth rate of filter-feeding invertebrates is significantly greater in otter-dominated ecosystems because of the resulting increased production and availability of particulate organic carbon in coastal waters (Duggins et al. 1989). Kelp forest fish populations are enhanced in otter-dominated ecosystems (Reisewitz et al. 2006), and thus the diet and foraging behavior of other fish-eating species is altered by the presence or absence of sea otters. These effects have been well-documented in areas of Alaska where contrasts between otherwise similar ecosystems with and without sea otters have been possible (Estes et al. 1996, 2005). It is important to recognize that while the direct effects of sea otter predation are reasonably well documented and thus well-known, the indirect effects of sea otter predation are diverse and complex, and thus the majority of these potential indirect effects remain unstudied and unknown.

### Sea otters and coastal ecosystems in southern California

The aforementioned synopsis of ecosystem effects by sea otter predation is founded on information obtained from more northerly areas—central California, Washington, British Columbia, and especially Alaska. Would similar ecosystem-level effects of sea otters be expected to occur in the Channel Islands and along the mainland coast of the southern California Bight? While that question cannot be answered with certainty, there are similarities and differences among these ecosystems that bear on the issue. Perhaps the most important difference between kelp forest ecosystems in southern California and those further north is that the southern California system is characterized by a greater diversity of macroinvertebrate herbivores and predators on those herbivores (Jackson et al. 2001, Steneck et al 2003). Whereas sea urchins are the dominant large grazer in Alaskan waters (Steller's sea cows are now extinct), southern California kelp forests support at least 3 common urchin species, at least 5 species of abalones, and several potentially important herbivorous fishes. And whereas sea otters (and predatory starfish in some areas) are the only known significant predators on these invertebrates in Alaska, several other important predators occur in southern California, including benthic predatory fishes and spiny lobsters. Furthermore, southern California kelp forests occasionally are physically disturbed by strong El Niño/La Niña events, effects that apparently are of lesser importance in more northerly kelp forest ecosystems. As a consequence of this increased diversity of biological and physical processes in southern California, southern California kelp forests probably did not respond as dramatically to the loss of sea otters as their Alaskan counterparts. Predictions of all the ways in which this system might respond to the reestablishment of sea otters is similarly difficult. A thorough discussion of these complex issues is beyond the scope of our intent for this

white paper. The following, however, is a brief synopsis based on our current knowledge and perspectives.

## Status of kelp forest ecosystems in southern California

Except for the colony at San Nicolas Island, seasonal migrants to the mainland coast south of Point Conception, and occasional vagrants that apparently wander south from central California, sea otters have been absent from southern California for more than a century. Various other species in this system have been substantially reduced by human exploitation or currently are in decline. Unfortunately, most of these reductions and declines are not well chronicled. A wide variety of reef fishes apparently have been reduced through recreational and commercial harvest (Dayton 2003). This includes a benthic feeding labrid, the sheephead, a functional analogue and potential competitor with sea otters. Other once-common species, such as the giant seabass, are now seldom seen. Abalone stocks have collapsed to such a low point that take of all kinds is now prohibited. Red sea urchins have been depleted in some areas, although a fishery for this species continues. There is also an apparently sustainable fishery for spiny lobsters.

Diseases figure prominently in the current ecology of southern California kelp forest ecosystems. Black abalone populations, extremely abundant in many areas of southern California until the 1980s or early 1990s, have collapsed throughout the region because of a chronic wasting disease (Lafferty and Kuris 1993, Altstatt et al. 1996). Purple sea urchin populations undergo periodic disease outbreaks, transforming some habitats from urchin barrens to kelp forests. Long-term records from the USGS kelp forest monitoring program at San Nicolas Island suggest that the ecosystem has transitioned into a state of chaotic oscillation over the past several decades. The data indicate that sea urchin populations increase to extremely high levels now that their most significant predators and competitors have been depleted, apparently facilitating in turn the spread of disease through the urchin populations and thus causing urchin populations to collapse. Kelps recruit rapidly after the urchin declines and the process then runs another cycle. Although this scenario remains hypothetical, there is independent evidence from the northern Channel Islands that the frequency and intensity of the urchin disease outbreaks are positively correlated with sea urchin population density, which in turn is negatively related to sheephead and lobster abundance (Lafferty 2004). These findings suggest that the dynamics of southern California kelp forest ecosystems may have come increasingly under the control of disease-limitation as natural predators have been reduced and the abundance of their prey has grown to abnormally high levels.

#### Direct effects of sea otters on southern California shellfisheries

The reestablishment of sea otters in southern California waters almost certainly will have negative impacts on shellfisheries. Sessile species that occur primarily in shallow water (such as abalones and sea urchins) are especially likely to be negatively impacted by sea otter predation. The effects of otters on other fisheries, such as the warty sea cucumber, are less certain, although stocks of this species appear to be in decline due to the intensity of fishing effort (Schroeter et al. 2001). The effects of sea otters on spiny lobster

populations are also uncertain. Although the sea otters at San Nicolas Island are known to prey on lobsters, lobsters may be less vulnerable to sea otters because of their mobility. Overall, however, the influence of sea otters on invertebrate and shellfisheries will be negative.

## Indirect effects of sea otters on southern California ecosystems

As is clearly the case elsewhere, significant indirect effects of sea otter predation should be expected for southern California kelp forest ecosystems. For instance, it is unlikely that sea urchin barrens will develop or persist in areas supporting significant numbers of sea otters. Overall, the distribution and temporal stability of kelp forests should increase with the spread of sea otters into southern California. Potential sea otter competitors, such as sheephead, may be negatively affected because of reductions in the abundance of their common benthic invertebrate prey. Populations of other kelp forest fish species (e.g., surfperch, rockfish, kelp bass) that depend on kelp as a source of habitat or food will likely increase. The importance of disease in regulating certain shellfish populations might be expected to decline as infectious disease transmissibility across individuals declines with declining population densities (and increasing average distances across individuals).

## Document Updates

There are 3 significant background documents that have been prepared by or for FWS that pertain to the management and conservation of sea otters in California—the Reinitiation of Formal Consultation on the Containment Program for the Southern Sea Otter (released 8 January 1999); the Final Revised Recovery Plan for the Southern Sea Otter (published 24 February 2003); and the Draft Supplemental Environmental Impact Statement: Translocation of southern sea otters (released October 2005). Because these various documents are now dated to varying degrees, some of the information they contain is not current. The final section of this white paper provides corrections and updates of key scientific information in these documents, as of January 2006.

Reinitiation of Formal Consultation on the Containment Program for the Southern Sea Otter

Page 18, para 3. The most recent and comprehensive estimate of carrying capacity (and thus historical abundance) of sea otters in California waters (Laidre, K. L., R. J. Jameson, and D. P. DeMaster. 2001. An estimation of carrying capacity for sea otters along the California coast. Marine Mammal Science 17:294-309) is closer to 16,000 individuals.

Page 19, para 2. As pointed out above, the conclusion that the California sea otter population is stationary or in decline is dated and incorrect. The most recent survey data indicate that overall population abundance is currently increasing.

Page 20, para 3. The overview of the status and trends of sea otters at San Nicolas Island is dated. Current data indicate that the population at San Nicolas increased from about 1999 through 2003 but has since stabilized or declined (see narrative above).

Page 20, para 4. The information referred to in this paragraph is now published (Estes et al. 2003, cited below).

Page 21, para 1. More recent analyses indicate that the likelihood of detecting one or more drowned sea otters in pots and fish traps, even if the loss rate is relatively high and with a fairly intensive monitoring effort, is very low (Estes and Tinker, unpublished analyses).

Page 21, para 5. Current evidence supports the food-limitation or density-dependent hypothesis of population regulation in California sea otters (see above narrative).

Page 22. More recent information obtained from TDR (time-depth recorder) records indicate that California sea otters commonly dive to depths greatly in excess of 25 m. The maximum dive depth as determined from TDR records in Alaska and California now appears to be about 100m.

Page 31 (top). The conclusion that the southern sea otter population is in decline is dated. A more current analysis of the data indicates that the population is increasing (see section entitled <u>Population Trends—Central California</u>, P.2 above).

Page 32, para 3. The statement that male sea otters in the Aleutian Islands do not defend territories is incorrect. The existence of territorial males has been well documented in more recent studies of marked animals at Amchitka and Adak islands.

Page 33, para 4. There is now information that nutritional limitation is acting on sea otters in central California. This finding lends further support to the contention in the subject passage that moving males into the current range from southern California would exacerbate nutritional stress on the overall population.

Page 35, para 1. The claim that relocations back into the current range in central California would likely decrease birth rate is probably incorrect. The available evidence indicates that birth rates in sea otters do not vary in response to environmental factors of any kind.

Final Revised Recovery Plan for the Southern Sea Otter

Except for the updates provided in the narrative section of this white paper, this material is correct and current as written.

Draft Supplemental Environmental Impact Statement: Translocation of southern sea otters

Since this material was prepared recently, the discussion and conclusions are generally accurate, current, and complete. The discussion of ecosystem-level impacts, while

necessarily speculative, is thorough and generally accurate, although some additional thoughts and comments are provided in the narrative section of the white paper.

#### References

- Alstatt, J.M., R.F. Ambrosc, J.M. Engle, P.L. Haaker, K.D. Lafferty, and P.T. Raimondi. 1996. Recent declines of black abalone *Haliotis cracherodii* on the mainland coast of central California. Marine Ecology Progress Series 142:185-192.
- Bentall, G.B. 2005. Morphological and behavioral correlates of population status in the southern sea otter: a comparative study between central California and San Nicolas Island. Master's Thesis, University of California, Santa Cruz, CA
- Carpenter, S.R. and J.F. Kitchell (eds.). 1993. The Trophic Cascade in Lakes. Cambridge Univ. Press, New York.
- Dayton, P.K. 2003. The importance of the natural sciences to conservation. The American Naturalist 162:1-13.
- Duggins, D.O., C.A. Simenstad, and J.A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170-173.
- Estes, J.A. 1996. The influence of large, mobile predators in aquatic food webs: examples from sea otters and kelp forests. Pp.65-72 in S.P.R. Greenstreet and M.L. Tasker, eds., *Aquatic Predators and their Prey*. Fishing News Books, Oxford.
- Estes, J.A. 2005. Carnivory and trophic connectivity in kelp forests. Pp. 61-81 in, J.C. Ray, K.H. Redford, R.S. Steneck, and J. Berger (eds.). Large carnivores and the conservation of biodiversity. Island Press, Washington, D.C.
- Estes, J. A., B. B. Hatfield, K. Ralls, and J. Ames. 2003. Causes of mortality in California sea otters during periods of population growth and decline. Marine Mammal Science 19:198-216.
- Estes, J.A., E.M. Danner, D.F. Doak, B. Konar, A.M. Springer, P.D. Steinberg, M.T. Tinker, and T.M. Williams. 2004. Complex trophic interactions in kelp forest ecosystems. Bulletin of Marine Sciences 74:621-638.
- Gerber, L. R., T. Tinker, D. Doak, and J. Estes. 2004. Mortality sensitivity in life-stage simulation analysis: A case study of southern sea otters. Ecological Applications 14:1554–1565.
- Hatfield, B. B. 2005. The translocation of sea otters to San Nicolas Island: an update. In D.K. Garcelon and C.A. Schwemm eds., Proceedings of the Sixth California Islands Symposium, Ventura, California, December 1-3, 2003.
- Hebblewhite, M., C.A. White, C.G. Nietvel. J.A. McKenzie, T.E. Hurd, J.M. Fryxell, S.A. Bayley, and P.C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86:2135-2144.

- Jackson, J.B.C., M.X. Kirby, W.H. Berger, K.A.Bjorndal, L.W.Botsford, B.J. Bourque, R. Bradbury, R. Cooke, J.A. Estes, T.P. Hughes, S. Kidwell, C.B. Lange, H.S. Lenihan, J. M. Pandolfi, C.H. Peterson, R. S. Steneck, M.J. Tegner, and R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-638
- Kreuder, C., M. A. Miller, D. A. Jessup, L. J. Lowenstine, M. D. Harris, J. A. Ames, T. E. Carpenter, P. A. Conrad, and J. A. K. Mazet. 2003. Patterns of mortality in southern sea otters (*Enhydra lutris nereis*) from 1998-2001. Journal of Wildlife Diseases 39:495-509.
- Kreuder, C., M. A. Miller, L. J. Lowenstine, P. A. Conrad, T. E. Carpenter, D. A. Jessup, and J. A. K. Mazet. 2005. Evaluation of cardiac lesions and risk factors associated with myocarditis and dilated cardiomyopathy in southern sea otters (*Enhydra lutris nereis*). American Journal of Veterinary Research 66:289-299.
- Lafferty, K. D. 2004. Fishing for lobsters indirectly increases epidemics in sea urchins. Ecological Applications 14:1566-1573
- Lafferty, K.D. and A.M. Kuris. 1993. Mass mortality of abalone *Haliotis cracherodii* on the California Channel Islands: tests of epidemiological hypotheses. Marine Ecology Progress Series 96:239-248.
- Mayer, K. A., M. D. Dailey, and M. A. Miller. 2003. Helminth parasites of the southern sea otter *Enhydra lutris nereis* in central California: Abundance, distribution and pathology. Diseases of Aquatic Organisms 53:77-88.
- Miller, M. A., I. A. Gardner, C. Kreuder, D. M. Paradies, K. R. Worcester, D. A. Jessup, E. Dodd, M. D. Harris, J. A. Ames, A. E. Packham, and P. A. Conrad. 2002. Coastal freshwater runoff is a risk factor for *Toxoplasma gondii* infection of southern sea otters (*Enhydra lutris nereis*). International Journal for Parasitology 32:997-1006.
- Miller, M. A., M. E. Grigg, C. Kreuder, E. R. James, A. C. Melli, P. R. Crosbie, D. A. Jessup, J. C. Boothroyd, D. Brownstein, and P. A. Conrad. 2004. An unusual genotype of *Toxoplasma gondii* is common in California sea otters (*Enhydra lutris nereis*) and is a cause of mortality. International Journal for Parasitology 34:275-284.
- Pace, M.L., J.J. Cole, S.R. Carpenter, and J.F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14:483-488.
- Paine, R.T. 1980. Food webs: linkage, interaction strength, and community infrastructure. J. Anim. Ecol. 49:667-685.
- Ray, J.C., K.H. Redford, R.S. Steneck, and J. Berger (eds.). 2005. Large carnivores and the conservation of biodiversity. Island Press, Washington, D.C.

- Reisewitz, S.E., J.A. Estes, and S.A. Simenstad. 2006. Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian archipelago. Oecologia 146: 623-631.
- Ricdman, M.L., and J.A. Estes. 1990. The sca otter (*Enhydra lutris*): behavior, ecology, and natural history. Biological Report 90(14), U.S. Fish and Wildlife Service. 126pp.
- Schmitz, O.J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic Cascades in terrestrial systems: a review of the effects of carnivore removals on plants. American Naturalist 155:141-153.
- Schroeder, S.C., D.C. Reed, D.J. Kushner, J.A. Estes, and D.S. Ono. 2001. The use of marine reserves in evaluating the dive fishery for the warty sea cucumber, *Parastichopus parvimensis* in California, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 58:1771-1781.
- Soulé, M.E., J.A. Estes, J. Berger, and C. Martinez del Rio. 2002. Recovery goals for ecologically effective numbers of endangered keystone species. Conservation Biology 17:1238-1250.
- Soulé, M.E. and J. Terborgh (eds.) 1999. Continental Conservation, Island Press, Washington, D.C
- Steneck, R. S., M.H. Graham, B.J. Bourque, D. Corbett, J.M. Erlandson, J.A. Estes, and M.J. Tegner. 2003. Kelp forest ecosystem: biodiversity, stability, resilience and future. Environmental Conservation 29:436-459.
- Terborg, J., L. Lopez, P. Nunez V., M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascinio, G.H. Adler, T.D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923-1926
- Tinker, M. T. 2004. Sources of variation in the foraging behavior and demography of the sea otter, *Enhydra lutris*. Ph.D dissertation, University of California, Santa Cruz.
- Tinker, M. T., D. F. Doak, J. A. Estes, B. B. Hatfield, M. M. Staedler, and L. Bodkin James. *in press*. Estimating spatial and temporal variation in the demography of southern sea otters. Ecological Applications
- Tinker, M.T., D. F. Doak, and J. A. Estes. *in review* (Conservation Biology). Using demography and movement behavior to predict range expansion of the southern sea otter.