Fundamental to the conservation and management of wildlife resources is an understanding of a population's status, both in terms of abundance relative to its naturally occurring equilibrium level or carrying capacity, and rate of change (Caughley 1977; Eberhardt and Siniff 1977). A variety of criteria for determining the status of wildlife populations have been suggested (Eberhardt and Siniff 1977; Hanks 1981; Fowler and Siniff 1992), and are summarized in Table 1. Proposed criteria include both direct measures, such as the ratio of current abundance to carrying capacity abundance, and indices, such as time-activity budgets or body condition, that may be indicative of population status. Routine monitoring of population status improves management capabilities and may be particularly relevant to resource conservation.

Table 1. Summary of indices proposed to estimate the status of a population relative to an equilibrium level (after Hanks 1981; Fowler and Siniff 1992). Techniques applied to sea otters are in italics.

<table>
<thead>
<tr>
<th>Population Parameters</th>
<th>Physiological Parameters</th>
<th>Behavioral Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Distribution</td>
<td>1. Growth rates and individual size</td>
<td>1. Time activity budgets</td>
</tr>
<tr>
<td>2. Rate of change</td>
<td>2. Serum chemistry and hematology</td>
<td>2. Territory size</td>
</tr>
<tr>
<td>5. Survival rates</td>
<td>5. Parasites</td>
<td>5. Food habits</td>
</tr>
<tr>
<td></td>
<td>7. Adrenocortical hypertrophy</td>
<td></td>
</tr>
<tr>
<td></td>
<td>8. Urinary excretion of hydroxyproline</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9. Developmental stability (asymmetry)</td>
<td></td>
</tr>
</tbody>
</table>

Due to the recent history of exploitation and recovery (see Anderson et al.; Estes et al., this issue) and the resulting spatial separation of populations, sea otters in the north Pacific provide a unique opportunity to evaluate techniques for monitoring population status. Within the current range of sea otters,
populations exist that have been at or near equilibrium density for as long as 50 years (e.g., Architka, Alaska; see Figure 1).

![Map of the northern Pacific Ocean showing some sea otter populations near equilibrium density and others below equilibrium density.](image)

Other populations have recently attained equilibrium density (e.g., Bering Island, Russia and Prince William Sound, Alaska) while others remain below (e.g., Olympic Peninsula, Washington; Vancouver Island, British Columbia; and Southeast Alaska). The status of the mainland California population apparently remains uncertain. The known variation in status among populations, a well described natural history, and the relative ease of enumerating sea otters provide a solid foundation for testing techniques to estimate sea otter population status. The results of research aimed at evaluating sea otter population status may be transferable to other wildlife populations, including endangered species, which are not as readily studied. Our purpose in this paper is to describe those measures of population status that have been applied to sea otters (see Table 1), discuss their relative merits, and recommend directions for research that may improve our ability to accurately monitor sea otter population status.

**Population parameters**

**Distribution**

Observations of animals reoccupying areas they had historically inhabited, or of vacant habitat where they were previously present, is a clear indication of population change. Available information suggests that the distribution of otters remains fairly stable over decadal time scales in equilibrium populations such as Amchitka, although abundance may vary, but that seasonal shifts may be pronounced and possibly predictable. Change in distribution in growing populations appears less predictable, particularly in areas of complex coastal physiography, such as southeast Alaska, compared to populations occupying more linear coastlines, such as California. Accurately describing changes in distribution requires systematic population surveys that should include areas adjacent to occupied habitat.

**Rate of change**

Population status may be inferred from the direction and rate of change in numbers in a population. Rate of change, resulting from the balance between recruitment and mortality, likely reflects a response to prior conditions rather than present, or future conditions. However, alterations in the rate of change might provide some predictive power (e.g., a population that continues to grow, but at a decreasing rate, may
be approaching equilibrium). Generally, remnant populations have experienced slower growth rates than
translocated populations, or naturally recolonized islands (Estes 1990a; Bodkin, unpublished data).
Annual growth rates observed from several remnant populations range from about 5% (California) to 6-
8% (Prince William Sound and Kodiak) to 13% at Amchitka, compared to about 20% consistently
observed for translocated populations in Southeast Alaska, Washington and British Columbia.

Several types of data can be used to calculate rate of change. These are summarized below, with assets
and liabilities noted for each.

**Measures of abundance**

*Estimates of relative abundance.* Counts of sea otters have been made from shore, skiffs, larger boats, a
variety of fixed-wing aircraft, and helicopters, or a combination of these. It has been generally recognized
that some proportion of the population is not observed during surveys. In Prince William Sound, Udevitz
et al. (1995) demonstrated that 30% of the sea otters present were missed during skiff surveys, because
of avoidance by otters and failure to observe otters present.

It is likely that detection probabilities differ among surveys, even if methods are similar. Average sea otter
detection probabilities from fixed wing aircraft were <0.50 and varied widely both within and among
observers (Bodkin and Udevitz 1996; Bodkin, unpublished data). Consequently, if indices of abundance
are to provide unbiased estimates of the proportional change in a population, the probability of detecting
otters must be known for each survey. However, estimating detection probability can be difficult, and most
surveys do not account for undetected otters, complicating comparisons among surveys.

*Estimates of absolute abundance.* Estimating absolute sea otter abundance through systematic sampling
requires a method to estimate the proportion of animals not detected while sampling. Bodkin and Udevitz
(1996) have developed an aerial survey method consisting of a strip transect design where all otters
observed in a 400 m wide strip on one side of an aircraft are counted. The proportion of otters not seen is
estimated by conducting intensive searches within the strip transects. A similar procedure was attempted
from helicopters in Alaska (DeGange et al. 1995). The aerial methodology should be validated in a
population of known size, and may provide additional information on the California population.

Estimates of absolute abundance can be important in population management. For example, sea otter
abundance data would have been of great value in determining the magnitude of mortality from the 1989
Exxon Valdez oil spill (Ballachey et al. 1994; see Bonnell et al., this issue).

**Population census**

Counts of sea otters from the shore have generally been recognized as the most accurate means of
enumerating sea otter abundance. Estes and Jameson (1988) estimated the detection probability of sea
otters using standardized shore counts at 94.5%. This was the first rigorous evaluation of this survey
method, and provided a baseline against which other methods could be tested. Due to access
constraints, however, shore-based counts have limited application over the large areas occupied, or
potentially occupied, by many sea otter populations.

In California, a combination of a census (ground count) and index of abundance (aerial counts) are
combined to provide annual minimum counts. These counts are biased low to the extent that each
method does not account for animals not detected. To retain comparability over time (assuming relative
abundance remains constant), it will be important to continue using each method proportional to its use in
previous surveys.

**Population density**
Assuming equilibrium densities are similar among similar habitats, density estimates should provide an objective and direct measure of population status. Following complete reoccupation, about 50 years ago, a decline in density was observed at Amchitka Island (Kenyon 1969). In 1991 at Bering Island, a 40% reduction in sea otter density was observed following complete reoccupation of the island during the 1980s (A. Burdin, unpublished data). Estes (1990a) used densities to evaluate the recovery of sea otters at Attu Island. Comparison of densities between Attu and Amchitka Island led Estes (1990) to develop a hypothesis regarding multiple equilibria, where sea otter densities reached a second, higher equilibrium density, following a diversification of diet. The possibility of multiple equilibria should be considered in interpreting trends in population density.

Estimation of density requires delineating suitable habitat accurately. Potential sea otter habitat can be defined from the high intertidal to a bathymetric contour beyond which sea otters cannot forage due to diving limitations. Our data from Prince William Sound suggest that sea otters between the shoreline and the 200 m contour interval are not evenly distributed. Approximately 80% of the otters observed on surveys between the shoreline and the 200 m contour were within the 40 m contour interval, which is about a third of the total area. Until the relation among the distribution of substrate depths, habitat characteristics, and sea otter density is defined, the use of density to compare populations should be limited to areas of similar bathymetry and habitat. Data on the distribution of dive depths of individual otters may prove useful in describing this relation. Additionally, a potential relation between diving depths and population status may exist.

Indices of density will result if the survey method does not estimate the proportion of sea otters not detected (Udevitz et al. 1995). Valid comparisons across or within populations using an index require the assumption that detection probabilities do not differ among surveys. It is unlikely that this assumption is valid. If detection probabilities can be estimated, unbiased estimates of abundance will result. The results of a complete census or an unbiased estimate of abundance will result in unbiased density estimates that should be comparable within and among populations.

Reproduction

Two specific reproductive attributes have been proposed as indices of sea otter population status: age at first reproduction and age-specific reproductive rates. Most studies to date have found relatively consistent results among populations in these variables. Generally, a small proportion of female sea otters reproduce at age 2, most are mature by age 4, and age-specific rates are relatively high and consistent among mature females (Riedman and Estes 1990; Jameson and Johnson 1993; Bodkin et al. 1993; Monson and DeGange 1995; Monson 1995).

Reproductive characteristics in female sea otters have been studied through analysis of reproductive tracts and monitoring known individuals. Tract analysis requires carcasses in good condition, which usually are not available in large numbers. Monitoring known individuals has been accomplished most efficiently with the aid of radio telemetry. Adult female reproductive rates are generally high (0.80-0.94) among those populations sampled (Schneider 1973; Jameson and Johnson 1993; Siniff and Ralls 1991; Bodkin et al. 1993; Monson and DeGange 1995; Monson 1995), and include estimates from populations of differing status (California, Amchitka, Prince William Sound and Kodiak). However, reproductive rates appear to vary among ages, leading to the need to restrict comparisons to similar ages. Much less work has been done on aspects of male reproductive biology, although sperm samples collected in Prince William Sound indicate that males may attain maturity as early as age 3 (Ballachey, unpublished data). In summary, it appears that the reproductive characteristics studied to date are relatively invariant, and therefore unlikely to provide a sensitive index to population status.

Survival rates

Survival rates, particularly of juveniles, have been suggested as the life history variable most sensitive to environmental conditions (Eberhardt 1977; Hanks 1981). Annual survival rates among adult sea otters
Juvenile sea otter mortality can be evaluated in two components: through dependency, and after weaning. Dependent juvenile survival has generally been estimated by following known females from pupping through weaning. Comparisons of pre-weaning survival rates suggest variability among populations. Estimates from California are 0.46 (Siniff and Ralls 1991), 0.64 (Jameson and Johnson 1993) and 0.60 (Riedman et al. 1994); and from Alaska are 0.85 at Kodiak Island (Monson and DeGange 1995), and 0.29 and 0.54 at Amchitka (Monson 1995).

Post-weaning juvenile survival rates estimated from Prince William Sound are 0.32-0.51 for males (Monnett 1988). Post-weaning survival was an estimated 0.08 (males) and 0.21 (females) in 1990/91 (Rotterman and Monnett 1991) and 0.47 (males) and 0.59 (females) in 1992/93 (National Biological Service, unpublished data) in western Prince William Sound. During the same periods of study survival rates in eastern Prince William Sound were 0.33 (males) and 0.43 (females) in 1990/91 and 0.42 (males) and 0.89 (females) in 1992/93. At Amchitka, only 2 of 11 (0.18) pups survived one year post-weaning (Monson 1995). These data suggest that juvenile survival rates are lowest in populations that may be considered at or near equilibrium, and highest in growing populations such as Kodiak. Post-weaning juvenile survival appears to be highly variable among years, as well as within sub-populations, based on the Prince William Sound data. The Prince William Sound data are difficult to interpret because, in studies to date, potential oil effects cannot be separated from potential area effects related to differences in length of occupancy. However, if we assume no chronic oil spill effect, the comparisons between western and eastern Prince William Sound suggest juvenile survival may be a sensitive index of population status. Additionally, the large inter-annual variation observed in juvenile survival suggests we question the assumption of a stable age distribution in sea otter populations (Eberhardt and Siniff 1988; Monson 1995).

Physiological parameters

Although physiological measures of population status have been considered for many years (Hanks 1981; Fowler and Siniff 1992), the 1989 Exxon Valdez oil spill in 1989 in Prince William Sound provided a major impetus to evaluate health of (1) individual sea otters captured for treatment and release and (2) the wild population, for indications of continuing deleterious effects of the spill. Examinations of oiled sea otter carcasses demonstrated that exposure to oil (based on contamination of the fur) was associated with liver and kidney damage (Lipscomb et al. 1993, 1994). The question remained, however, whether sea otters in oiled areas would have poorer survival rates and, if so, the time until health and survival rates returned to pre-spill, normal values. To evaluate oil-related population damage and recovery, a series of studies on sea otters were implemented, primarily in Prince William Sound (Ballachey et al. 1994). These studies are still ongoing (see the NVP project, below), and may provide insight into new approaches for assessing population status.

Growth rates and individual size
Kenyon (1969) first described differences in weights and lengths of sea otters from growing and equilibrium sea otter populations. Results of recent research in Russia, Amchitka and Prince William Sound suggests that body condition (generally measured as the ratio of weight to length) may be useful as an indicator of population status. For example, between 1980 and 1989 the Bering Island population grew at >20% annually, but by 1990 it had apparently exceeded carrying capacity, as a large scale mortality event occurred during 1990/91. During this period of population growth, the mean weight of adult male carcasses declined significantly at Bering Island (Bodkin and Burdin, unpublished manuscript). In 1990, weights of adult males at Bering Island did not differ from weights of adult males collected in Prince William Sound, a population at or near equilibrium density. The number of otters at Bering Island has apparently stabilized at or near the number that persisted following the 1990/91 mortality event.

Although sample sizes were small, Monson (1995) found differences in the condition of adult female otters between 1993 and 1994 at Amchitka Island. Corresponding differences in pre-weaning survival were also observed, with females in better condition experiencing greater weaning success. In eastern Prince William Sound, weights of mothers of pups surviving at least 1.5 years were significantly greater than those of mothers of pups that died prior to 1.5 years. Additionally, capture data suggest that animals in more recently occupied areas in the eastern Sound are slightly heavier than those in areas of the western Sound (National Biological Service, unpublished data). However, we cannot discount the potential of an oil spill effect in observed differences.

Review of the studies presented above suggest that the condition of animals in growing, as well as equilibrium populations may be a fairly sensitive index to short term changes in ecological conditions experienced by the population, and may vary on time scales suitable for predicting change in population growth. Measuring body condition is a relatively non-invasive and simple procedure. Additional research relating body condition to survival rates and changes in abundance may be justified.

**Serum chemistry and hematology**

Prior to the 1989 oil spill, blood values (hematology and serum chemistry) of California sea otters had been reported (Williams and Pulley 1983; Williams et al. 1992). Subsequently, blood data have been obtained on additional populations, primarily in Alaska (Rebar et al. 1995, 1996; National Biological Service, unpublished data). Differences have been identified between sea otter subpopulations in Prince William Sound (in western and eastern areas) in serum enzymes and levels of certain white blood cells (Rebar et al. 1996; National Biological Service, unpublished data), but the biological significance of these differences at either the individual or population level is equivocal. Blood samples have been collected from several other sea otter populations in different stages of expansion. Comparison of blood values among populations, and relations with other measures of population status, should provide clarification of the utility of blood analyses for assessing populations.

**Immune response**

Immunological measures have been developed to screen populations for effects of toxic chemical exposure (Weeks et al. 1992). However, these techniques have not been applied to monitoring the status of wild populations when contaminants or disease are not a concern. Recent work in Prince William Sound demonstrated the feasibility of an in vitro lymphocyte proliferation assay using cells isolated from blood of wild-caught sea otters (P. Snyder, unpublished data); the technique is currently being applied to samples collected from Prince William Sound subpopulations to evaluate potential differences in status.

**Other**

Other body fluids (urine, semen) have been collected from sea otters in southeast Alaska, and Prince William Sound (Ballachey 1995; National Biological Service, unpublished data) but have not been analyzed in terms of their relationship to population status.
Parasites have been frequently observed in necropsies of sea otters, including infestations in carcasses recovered from high density areas at Amchitka (Rausch 1953) and Prince William Sound (National Biological Service, unpublished data). Although it may be anticipated that parasite loads might increase as densities increase, no published data exist on parasite levels in sea otter populations of differing densities, or on the effect of parasite loads on survival and, consequently, population growth.

As yet, the value of individual physiological measures as estimators of population status, and their variability across populations in different stages of growth, are undetermined. Although measures evaluated to date may not prove to be useful tools for predicting population status, they nevertheless should be valuable for assessing health of individuals and provide a tool for understanding factors that may be limiting population growth.

**Behavioral parameters**

**Time activity budgets**

Considerable effort has been allocated in evaluating time activity budgets as an index of sea otter population status (Loughlin 1979; Estes et al. 1982; Ribic 1982; Estes et al. 1986; Garshelis et al. 1986; Ralls and Siniff 1988; Estes 1990b; Garshelis et al. 1990; Ralls and Siniff 1990; Gelatt 1996). Although conclusions have been equivocal, there does appear to be a general positive relation between length of occupancy and the proportion of time individuals allocate to foraging. However, local environmental and seasonal effects potentially may confound comparisons among populations. Differences in activity budgets among age/sex and reproductive status, as well as, local environmental conditions, should be considered in comparisons among populations. Both the apparent lack of sensitivity as an index and the extensive effort required in its estimation will likely limit the application of time activity budgets as an index of sea otter populations.

**Food habits**

Relatively little work has been done relating sea otter food habits to population status. However, some generalizations may be warranted. Sea urchins appear to be a preferred prey item of otters reoccupying former habitat, and the proportion as well as the mean size of urchins in the diet apparently decline as length of occupation increases. Similar changes may occur with clams in soft sediment communities. Foraging on fish appears to be an attribute primarily of populations limited by resources, but may be observed throughout the Aleutian Islands. And lastly, there may be an increase in prey species diversity, as populations become food resource limited.

**The "NVP" approach**

In 1995, we (along with a large number of other scientists) initiated a study entitled "Mechanisms of Impact and Potential Recovery of Nearshore Vertebrate Predators" (the NVP study). The primary objective is to determine the status of the near-shore marine ecosystem in western Prince William Sound affected by the Exxon Valdez oil spill of 1989. Our approach is to compare population, physiological and behavioral parameters in four vertebrate predators, the harlequin duck, pigeon guillemot, river and sea otter, in oiled and nearby, unoiled portions of Prince William Sound, as indicators of the ecosystem’s status. For sea otters, we are estimating abundance and reproduction, body condition, blood chemistry and immune response, and foraging success and prey selection. In addition, we are comparing sizes of sea otter prey in areas where otter populations were reduced and in areas where they were not. Sea otter predation is widely recognized as limiting the larger size classes of some invertebrate prey, such as sea urchins and mussels (Riedman and Estes 1990). If sea otter populations are reduced, prey populations might be expected to respond by increasing in size. We are using this knowledge as a way to measure if the affected sea otter population in Prince William Sound has recovered. Assuming sea otter densities, relative to carrying capacity, are similar between oiled and non-oiled areas, we expect to see similar size distributions of prey. Sea otter recovery may be indicated by similar prey sizes.
The NVP study and other ongoing efforts analyzing and comparing measurements taken in sea otter populations in different stages of expansion (expanding vs. at equilibrium) will provide further assessment of the array of measures potentially available to monitor population status.

**Conclusion and recommendations**

Contemporary sea otter populations are generally recognized by their geographic isolation. Although a population may be perceived as "single" because of geographic considerations, it may not be homogeneous in terms of population status, particularly if available resources vary by location. Considerable variation in survival may exist among individuals if, for example, juveniles born in the center of a population's distribution had a greater distance to travel to unoccupied habitat than juveniles born in areas closer to the boundaries of the population's distribution (assuming that a greater distance traveled decreases the likelihood of survival). Consequently, when evaluating or implementing measures of population status, it may be prudent to consider the potential for within population variation in status, particularly as remnant populations increase in numbers and distribution. With this in mind we make the following recommendations.

1. Continued monitoring of population trends is critical. Standardized survey methodologies will accommodate comparisons across populations. Survey methodologies should be evaluated by sampling populations of known size. Unbiased estimates of abundance provide benefits in documenting magnitude when change occurs, particularly declines from events such as oil spills.

2. Our review of available data suggest that a relation exists between body condition and vital demographic variables, such as juvenile survival, that may predict change in population abundance. This potential relation warrants additional consideration.

3. At least three attributes of an index of status are desirable: a. the method should be sustainable over time; b. the index should predict change, both direction and magnitude; and c. the index should indicate cause of change (e.g. intrinsic vs extrinsic).

4. Develop an understanding of the fundamental processes that are structuring sea otter populations, including the potential relation between dispersal distance and population growth rates in expanding populations and factors constraining growth in equilibrium populations.

5. Continue evaluation of the relation between population status and indices using populations in differing stages of recovery as well as within populations over time. Consideration should be given to combinations of indices to improve our ability to assess population status.

**Literature Cited**


James Bodkin and Brenda Ballachey are with the National Biological Service, Alaska Science Center, 1011 E. Tudor Road, Anchorage, AK 99503.