QUANTITATIVE DETERMINATION OF OPTIMUM SUSTAINABLE POPULATION LEVEL

TIM GERRODETTE[1]

Southwest Fisheries Center Honolulu Laboratory,
National Marine Fisheries Service, NOAA,
2570 Dole Street, Honolulu, Hawaii 96822-2396

DOUGLAS P. DeMASTER

Southwest Fisheries Center La Jolla Laboratory,
National Marine Fisheries Service, NOAA,
P.O. Box 271, La Jolla, California 92038

ABSTRACT

Quantitative methods are reviewed and compared for determining whether a marine mammal population is at an optimum sustainable population (OSP) level, a management goal specified by the U.S. Marine Mammal Protection Act. Methods of OSP determination fall into two general types: those that require an estimate of a population's maximum net productivity level (e.g., the back-calculation method) and those that do not (e.g., dynamic response analysis). The two types differ in the data they require and in whether they determine OSP with respect to present or historical carrying capacity. Back-calculation and dynamic response analyses are compared using data on the California gray whale (Eschrichtius robustus). Marine mammal monitoring programs should be designed to detect trends in both the abundance of a population and its condition relative to carrying capacity, because both quantities are involved in the definition of OSP. The value of using both abundance and condition indices in an assessment is illustrated with data on the northern fur seal (Callorhinus ursinus).

Key words: back calculation, dynamic response analysis, management, Marine Mammal Protection Act, optimum sustainable population.

The U.S. Marine Mammal Protection Act (MMPA) of 1972 specified that each marine mammal population should be maintained at an "optimum sustainable population" (OSP) level. This phrase was somewhat vague because it lacked an operational definition in existing management terms. Nevertheless, the MMPA represented a fundamental change in marine mammal management by recognizing that all organisms live in necessary interdependence with each other, and that the value of a marine resource should not be measured by economic criteria alone.

[1] Present address: Southwest Fisheries Center, La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, California 92038.

Unfortunately, the new management perspective has been difficult to implement, not only because of insufficient knowledge of the biology and ecology of marine mammal species, but also an insufficient theoretical foundation. Biological resource management with an ecosystem perspective is a relatively new concept, whereas management based on the dynamics of single species has a longer history of development and application in fisheries and wildlife biology. In practice, management of marine mammals has relied on concepts of single-species population dynamics. The U.S. National Marine Fisheries Service has defined OSP as a population level between carrying capacity and the population size at maximum net productivity (Federal Register, 21 December 1976, 41FR55536). A key point is that the maximum net productivity level (MNPL) forms the lower boundary of OSP range. In practice, therefore, the problem of establishing whether a marine mammal population is "optimum" usually involves determining whether it is above its MNPL.

Qualitative measures of OSP status have been proposed and used on a preliminary basis in the past, but more rigorous and quantitative methods are needed. There is not at present, nor is there likely to be in the future, any single analysis that is best in all situations. The selection of an analysis always depends on the available data, which, in turn, depend on the biology of the species being managed. In addition, because marine mammals "combine the problems of inaccessibility common to fish populations with the variability in behavior characteristic of terrestrial mammalian species" (Eberhardt et al. 1979, p. 6), consideration of new ways of determining OSP status is severely constrained by the types of data we are able to collect.

This paper reviews and compares quantitative methods presently available for determining, within the present definition of OSP, whether a population is in OSP range. Because OSP determinations may be challenged by various interest groups, the determination procedures should be scientifically credible and legally defensible (Bean 1983). Our specific evaluations apply to marine mammals under U.S. jurisdiction only, but the discussion of general approaches being attempted has wider applicability as many countries implement new principles of management of living resources (Holt and Talbot 1978).

REVIEW OF CURRENT PROCEDURES

For many marine mammal populations, few harvest data are available, and traditional fisheries methods of estimating MNPL from catch records are of little help. This has led to some new approaches to determine whether a marine mammal population is in OSP range. For heuristic purposes, approaches to OSP determination may be divided into two types: those that require an estimate of MNPL and those that do not.

Methods Requiring an Estimate of MNPL

A direct approach to determining OSP status is to estimate MNPL for the marine mammal population in question and compare this number to the current

estimated population size. This approach depends on the data available to estimate present population size, carrying capacity, and MNPL as a fraction of carrying capacity.

Present population size—The present population size must be measured in the same units in which carrying capacity is measured. For marine mammals, this unit will usually be absolute numbers of animals but could be some relative measure correlated with population size.

Carrying capacity (maximum sustainable population)—As normally used in applied population dynamics, carrying capacity refers to an equilibrium population level under conditions of no harvest. Human activities which lead to habitat degradation or loss may reduce the carrying capacity. The intent of the MMPA, however, clearly was not to condone alteration of marine mammal habitat; a reduction in carrying capacity due to habitat degradation may lead to a marine mammal stock being classified as depleted. Consequently, in the context of OSP determination and as used in this paper, carrying capacity refers to an equilibrium population level before impact by man, either direct (through harvest or incidental killing) or indirect (through habitat degradation or harvest of predator, prey, or competitor species). Unfortunately, carrying capacity in this sense can be difficult to measure, because few marine mammal populations today have not been impacted by man in some way. Furthermore, the species of greatest concern are those that have declined through the influence of man.

The primary technique for estimating carrying capacity has been the back-calculation method. Important assumptions of this approach are that the historical population, before substantial impact by man, was at equilibrium and that the environment has not changed greatly. Under these conditions, a past population size may be taken as an estimate of current carrying capacity. Back calculation relies on a knowledge of the population dynamics of the species and has affinities with what is known as "cohort analysis" in the fisheries literature (Ricker 1975). Birth and natural mortality rates or their difference, the net recruitment rate, are used to project the population backwards in time. Known losses in the form of harvests or incidental kills are used at each time step to calculate previous population size. The back-calculation method was used to estimate carrying capacity for several dolphin (*Stenella* spp.) populations during the status-of-porpoise-stocks determinations of 1976 and 1979 (Smith 1983). Ohsumi (1976), Reilly (1981), Cooke (1986), and Lankester and Beddington (1986) conducted back-calculation analyses for gray whales (*Eschrichtius robustus*). Breiwick *et al.* (1981, 1984) used variations of this method, including a time lag to allow for the period between birth and vulnerability to harvest, to estimate the 1848 abundance of bowhead whales (*Balaena mysticetus*) in the North Pacific prior to commercial whaling.

Smith and Polacheck (1979) investigated the sensitivity of the back-calculation method. In general, the reliability of estimates of historical population size depends on the reliability of the estimates of all of the quantities required— vital rates, numbers killed by man, and present population size. Which of these quantities is most important to the accuracy of the carrying capacity estimate depends on how far back into the past we project the population and on the

relative importance of man-induced to natural mortality. The method would work well, for example, with a population that had suffered a relatively recent decline dominated by known losses. The method is less useful if incidental kills are not known (and thought to be substantial) or if the time of the pre-exploitation population level is so far in the past that the estimate of carrying capacity is heavily dependent on the values chosen for the (usually poorly known) vital rates.

The back-calculation method also requires the specification of a density-dependent function for the vital rates. The usual choice has been a generalized logistic formulation (Allen 1976, Gilpin *et al.* 1976). The calculations of Smith (1983) showed that estimates of carrying capacity could be quite sensitive, particularly at realistic maximum rates of increase, to the choice of the exponent in the generalized logistic function. Lankester and Beddington (1986) and Cooke (1986) questioned the internal consistency of the density-dependent function traditionally used by the International Whaling Commission with known population trends and catch history of the gray whale.

A second approach to estimating capacity would rely on the measurement of some limiting resource for the population, such as food supply or haul-out sites. The validity of such estimates depends on sufficient knowledge of the species' ecology to demonstrate that the resource in question will, in fact, be limiting. Demonstrating this limitation from first principles is a daunting challenge. Consider food. An estimate of carrying capacity based on food supply would depend, at a minimum, on a knowledge of prey abundance, dietary preferences, metabolic requirements, and energetic conversion efficiencies. Most are dynamic quantities that change with population level, age, location, and physiological condition, not static quantities that need only be measured once. Knowledge of dietary preferences, for example, should include the population dynamics of prey populations and alternate prey sources as preferred prey become scarce. Thus, estimating carrying capacity by a limiting resource may imply, in theory, a rather complete understanding of the whole ecosystem in which the marine mammal lives.

A simplified and more practical variant of this approach is to demonstrate that an unharvested population is at equilibrium within a portion of the range. If density is known for that area, carrying capacity may be estimated as the product of the density of animals at equilibrium and the total area of available habitat. Such calculations have been used for sea otters (*Enhydra lutris*) in Alaska and California (Kenyon 1969, Estes and Palmisano 1974), but problems of scale and measurement of available habitat may arise (J. A. Estes, in preparation. Growth patterns in sea otter populations. Institute of Marine Sciences, University of California, Santa Cruz, CA 95064).

MNPL as a fraction of carrying capacity—In the absence of harvest data and observation of the population's dynamics over a wide range of population sizes, this parameter is difficult to estimate for a particular species. For most marine mammals, we rely on theoretical models of population dynamics and on general patterns revealed by comparative studies to provide estimates of MNPL as a fraction of carrying capacity. According to the widely used logistic model, MNPL

is at half the carrying capacity. Eberhardt and Siniff (1977) suggested that the demography of marine mammals leads to an MNPL at more than half the carrying capacity and, hence, that the lower limit of OSP range might lie closer to carrying capacity than specified by the logistic model. Fowler (1981) expanded on this theme, using theoretical arguments and empirical evidence to draw a contrast between some organisms with short lives, high reproductive rates, and production curve peaks shifted to relatively low population levels (*e.g.*, most fish) and other organisms with long lives, low reproductive rates, and production curve peaks shifted to relatively high population levels (*e.g.*, marine mammals). Fowler (1984, 1988) further demonstrated, for a wide variety of organisms, a high correlation between MNPL as a fraction of carrying capacity and the logarithm of the rate of increase per generation. This correlation is an important development because it could allow us to predict the position of MNPL as a fraction of carrying capacity on the basis of population parameters that are independent of harvest information and do not require observing the population at a wide range of sizes. However, the intrinsic rate of increase and generation time of the species must still be estimated.

During the status-of-porpoise-stocks determinations of 1976, MNPL was considered to be in the range of 0.5–0.7 as a fraction of carrying capacity, whereas in 1979, a range of 0.65–0.80 was used (Smith 1983). Although these numbers were based on the best available data, the range for MNPL, combined with uncertainty in other parameters, allowed room for several possible inter-pretations and did not clearly settle whether some dolphin stocks had been depleted below OSP. This led to a search for alternative methods.

Methods Not Requiring an Estimate of MNPL

Goodman (1988) recognized that the minimum information required to make an OSP determination is simply whether the present population is above or below MNPL, and that this need not require actual estimates of MNPL or even the present population size. Although there may be some cases in which a population is temporarily above carrying capacity and not in OSP range, the more typical problem is trying to determine on which side of MNPL the population currently lies. The essence of this approach is to find a parameter related to population size that can indicate whether the population is above or below MNPL, without having to estimate that level itself. Let us call such a parameter an OSP measure.

Eberhardt and Siniff (1977) proposed 12 criteria for establishing a relative population level:

Behavioral attributes
    1) Antagonistic and/or displacement behavior
    2) Time spent in searching for food or in tending and feeding young
    3) Shifts in dietary components
Individual responses
    4) Physical condition, including growth rates
    5) Incidence of disease and parasitism

Reproductive characteristics
      6) Age at first reproduction
      7) Annual reproductive rates of mature females
Populational aspects
      8) Age structure
      9) Survival rates, especially of young
     10) Occupancy of marginal range
     11) Rate of change of population size
     12) Effects on habitat or food base

The way in which these criteria change with population size is usually apparent. For example, as a population nears carrying capacity, age at first reproduction should increase and individual growth rates should decrease. The magnitude and relative importance of the changes are far from obvious, however. As noted by Eberhardt and Siniff (1977), we do not know how to scale these criteria to population size. Their usefulness, therefore, is to indicate in a general way whether a population is near carrying capacity or far from it. This qualitative approach has been used previously by the National Marine Fisheries Service to assess many species of marine mammals when data on historical take were not available. Can any of the above criteria be sufficiently quantified to be used as an OSP measure?

Let us consider the desirable characteristics of an OSP measure. First, the OSP measure should be an easily measurable aspect of the population. Among the 12 criteria listed above, some are much easier to measure than others. Incidence of parasitism might be a good indicator of population status, but difficulties in measuring this parameter might preclude its use for many populations. A distinction also should be drawn among the above criteria according to whether they are individual or population measures. The first five criteria are measurable for an individual animal; provided variation for the character among individuals is not excessive, a sample of a few animals might suffice. The last seven criteria are population characteristics not defined for an individual. They require collection of an unbiased sample of a number of individuals, a more difficult type of datum to collect. Then again, certain criteria, such as dietary composition, disease, and occupancy of marginal range, might only require determining presence or absence. If such measures could be defined quantitatively in terms of an OSP level, they would have considerable appeal because of the relative ease of data collection.

A second desirable characteristic of an OSP measure is a highly consistent relationship to population size. Variance in the OSP measure should be small, allowing it to be used as a surrogate for population size. If there is no harvest or incidental take, the relationship of the measure to actual population size need not be known, because a relative scale is sufficient (Goodman 1988). The measure should also be uninfluenced by other conditions. If shifts in diet composition are used to indicate changes in population size, for example, they should depend on population size of the marine mammal only and not on changes in the relative abundance of different prey species.
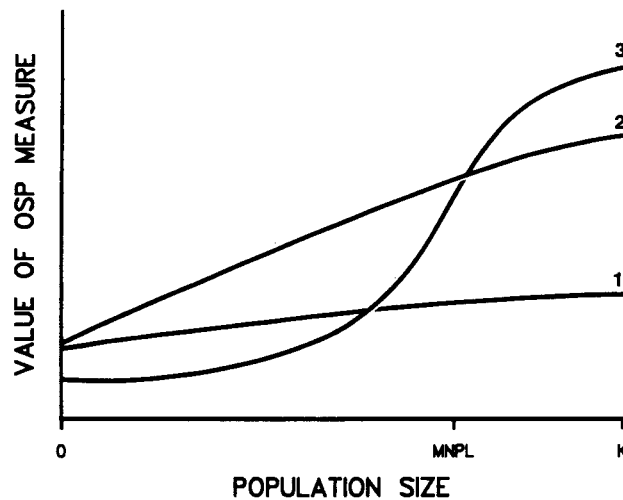
Figure 1. Hypothetical curves of three OSP measures as a function of population size.

Third, a practical OSP measure undergoes an easily detectable change as a function of population size. Even if easy to measure and tightly correlated with population size, an OSP measure will not be useful if the degree to which it changes with population size is small with respect to our ability to measure it (curve 1 in Fig. 1). Adult survival rates might be sensitive to population size, but the difference in survival rates between a population below its MNPL and one above its MNPL is probably too small for us to measure reliably. A more useful OSP measure would have a large range of values (curve 2 in Fig. 1), and its rate of change would be greatest in the vicinity of MNPL (curve 3 in Fig. 1).

Fourth and perhaps most critically, the value of the OSP measure above and below MNPL must be known so that the value can be related to an OSP level. This is a difficult requirement. For example, to be an OSP measure, the age at first reproduction that would indicate whether the species is above or below its MNPL must be specifiable. Although the trend of the indicator might be predictable (*e.g.*, an increasing age at first reproduction will accompany increasing population size), predicting a specific critical value *a priori* is beyond our present knowledge. It might be possible to discover empirically what ages at first reproduction indicate a population is below MNPL *if* there were some independent way, at the same time, of assessing population status relative to MNPL. But if there were this other independent measure, age at first reproduction would not have to be used. Thus, a critical value of an OSP measure as a function of population size will have to be predicted on theoretical grounds. Furthermore, to withstand legal scrutiny and challenge, the OSP measure must be based on a widely accepted model of population dynamics.

The technique available at present that most closely satisfies these four char-

acteristics is dynamic response analysis (Goodman 1988). Because the analysis depends only on the mild assumption of a unimodal production curve, it is based on a widely accepted feature of population dynamics. Moreover, its metric—acceleration or deceleration of population growth—undergoes a known change precisely at MNPL. From a theoretical viewpoint, this new method appears quite useful. The practical requirements for satisfactory performance with a non-harvested species are a sufficiently long and precise sequence of a population abundance index (Gerrodette 1988). Dynamic response analysis has been used with the California sea lion (*Zalophus californianus*) (DeMaster *et al.* 1982) and northern elephant seal (*Mirounga angustirostris*) (Boveng *et al.* 1988).

Comparison of Two Methods to Assess OSP Status

Reilly (1981) performed numerous back calculations for gray whales. The simulation using historical (*ca.* 1800) carrying capacity of 24,000 whales resulted in a population trajectory that agreed most closely with the known history and exploitation of the species. In 1980, an estimated 15,647 gray whales comprised the North American population (Reilly *et al.* 1983). Thus, according to this analysis, gray whales in 1980 were about 65% of their historical maximum sustainable level, a figure placing them presumably at the lower end of OSP range.

We carried out a dynamic response analysis (see Boveng *et al.* (1988) for a description of methods) on gray whales for the period 1967–80, using the 13 yr of population estimates in Reilly *et al.* (1983). The pattern formed by plotting the second-order coefficients for a series of polynomial regressions against time (Fig. 2) is indicative of a population that initially (1967) was below MNPL and at the end (1980) was above MNPL. Most of the second-order coefficients were not significantly different from 0, but the pattern using 6–11 census periods was consistent: Coefficients were positive, declined to a minimum less than 0, then increased but usually remained negative (Fig. 2). Therefore, according to this analysis also, the California gray whale population was in OSP range in 1980.

This comparison provides compelling reasons for researchers to design their monitoring programs to collect, if possible, data needed to perform both methods of OSP determination. An assessment based on two relatively independent methods is much stronger. Moreover, because different kinds of data are used, agreement or disagreement between the two methods may give additional insights. For example, the agreement between the two methods strengthens Reilly's (1981) conclusion that California gray whales were in OSP range. It also suggests that, because back calculation assesses the population relative to historical carrying capacity while dynamic response analysis assesses it relative to current carrying capacity, the maximum sustainable population of gray whales has not changed greatly in the last 180 yr.

Abundance Indices and Condition Indices

The definition of OSP involves the relation between two quantities: population size and carrying capacity. Both quantities may change. DeMaster (1984) pointed
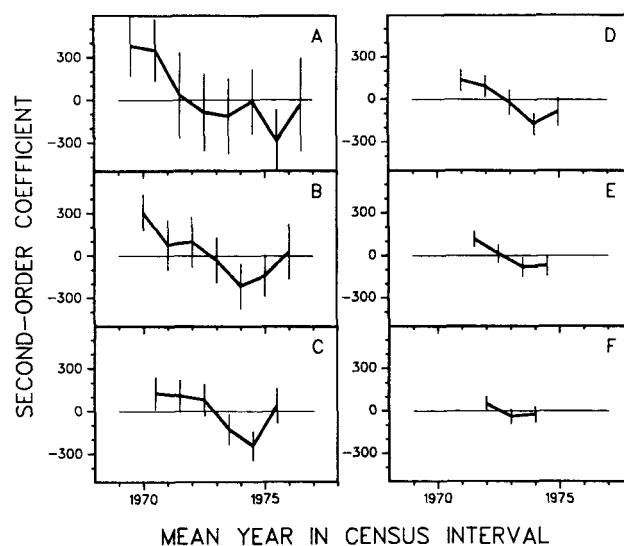
Figure 2. Dynamic response analysis for the California gray whale, 1967-80, using the method of Boveng *et al.* (1988). The second-order regression coefficient is plotted against the mean year in the sequence of censuses. Vertical bars are ±1 standard error. The different panels plot coefficients against sequences of censuses of different lengths. (A) 6 yr, (B) 7 yr, (C) 8 yr, (D) 9 yr, (E) 10 yr, and (F) 11 yr.

out that previous monitoring programs have confused abundance indices with condition indices. An abundance index measures an aspect of a population related to actual numbers of animals. Examples of abundance indices are number of pups or calves, number of territorial males, and number of sightings per kilometer. A condition index, on the other hand, measures the condition of a population relative to its resources. The 12 criteria of Eberhardt and Siniff (1977) listed above are condition indices.

A change in population size does not necessarily mean a change in OSP status, because carrying capacity might also have changed due to natural causes. Monitoring programs should therefore be designed to measure both abundance and condition indices. By knowing the trends in both types of indices, changes in carrying capacity may be deduced (Table 1). For example, if a condition index worsens, the population is nearer its carrying capacity, but if, at the same time, an abundance index has not changed, we may conclude that the carrying capacity of the environment for that species has declined (top center cell in Table 1). This is, no doubt, a simplistic way of viewing the complicated relations between a population and its environment, but it is surely less simplistic than assuming a constant environment.

The utility of monitoring both abundance and condition indices may be illustrated with the northern fur seal (*Callorhinus ursinus*). Of the numerous indices available for the Pribilof Islands population, we chose two as examples: number of pups born (an abundance index) and pup mortality rate on the rookery (a condition index). Both have declined over the last 16 yr (Fig. 3).

Table 1.   A decision matrix for determining changes in carrying capacity (*K*) indicated by changes in an abundance index and a condition index.

Condition index	Abundance index		
	Decrease	No change	Increase
Worse	K much lower	K lower	No change in K
No change	K lower	No change in K	K higher
Better	No change in K	K higher	K much higher

The decline in the abundance index could be ascribed to a reduction in carrying capacity; however, the declining pup mortality rate indicates that the population has been decreasing relative to its carrying capacity. The combination of changes in these two indices, therefore, is consistent with a population declining relative to a constant carrying capacity during this period (lower left cell in Table 1). The lack of change in carrying capacity is supported when the two indices are compared over a longer period. Pup mortality rate, as a function of number of pups born, has evidently been the same during recent years as it was early in the century when the population was at or below its present level (Fig. 4). Had carrying capacity declined, one would expect that the points for the last 16 yr (solid dots) would fall above points for earlier years, but this has not been the case.

DISCUSSION AND CONCLUSION

The current operational definition of OSP utilizes the concept, derived from fisheries management, of an MNPL. Confusion has sometimes arisen between MNPL and maximum sustainable yield (MSY) levels. Some authors have tried to use the MSY level as the lower boundary of OSP range (Bean 1983). This is unfortunate because the MSY level for a population is a function of its age structure as well as the age and sex composition of the harvest. The MSY level is undefined except in relation to a particular harvest; a population has no single MSY level. For example, if only pups are harvested, the MSY level for the Weddell seal (*Leptonychotes weddelli*) is 0.55 of carrying capacity, whereas if only adults are harvested, the MSY level is 0.69 (DeMaster 1981). By contrast, the MNPL is defined in the absence of a harvest as a function of the way birth and death rates change with density. The MNPL is usually taken to be that single level that would occur with no harvest, but if a harvest or other perturbation has displaced the population from a stable age and sex structure, there may be a different transient MNPL as the population recovers.

The need to regulate the take of marine mammals, particularly the incidental catch of *Stenella* spp. in the purse-seine tuna fishery, has stimulated the development of quantitative methods of OSP determination. Two general approaches have been attempted. One, exemplified by the back calculation of pre-exploitation dolphin population size in the eastern tropical Pacific (Smith 1983), requires the estimation of carrying capacity and MNPL. The other, represented
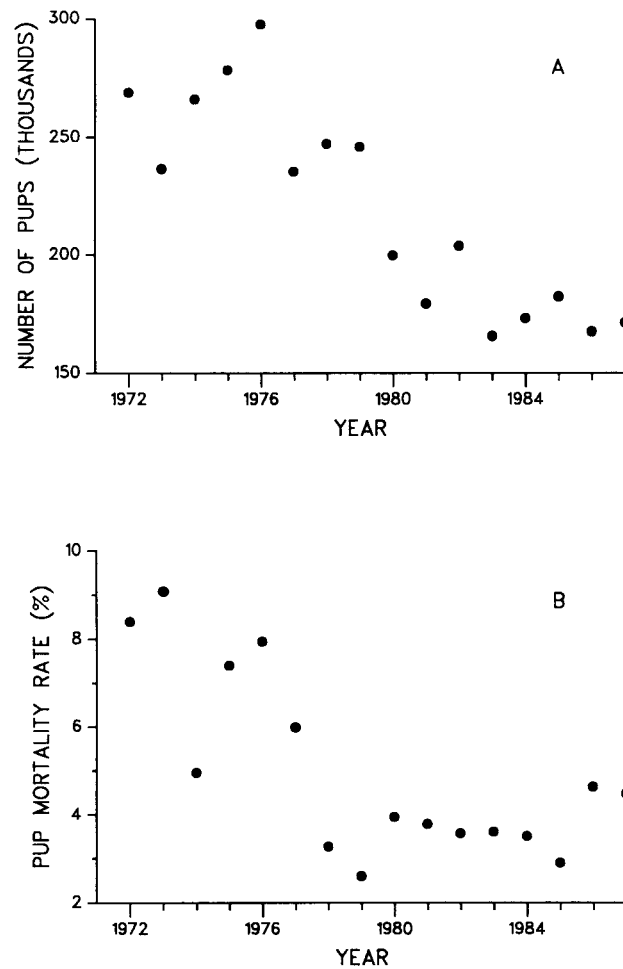
Figure 3. Trends in (A) births and (B) pup mortality rates for northern fur seals on St. Paul Island, Alaska, 1972–87. Data are from Lander (1980), York (1985), and, for recent years, unpublished records at the National Marine Mammal Laboratory, Seattle.

by dynamic response analysis (Goodman 1988), avoids the need to estimate carrying capacity and MNPL by considering the recent history of a population's dynamics. Which approach is more useful depends on the data available.

A dynamic response analysis requires a temporal sequence of an abundance index, augmented by data on mortality due to harvest or incidental kill. Because an estimate of population size (or at least an index of population size) is part of many monitoring programs, this type of datum may commonly be available. Whether such data are of sufficient number and precision for dynamic response analysis to be useful is a major question. For the precision of population estimates likely to be achieved with most marine mammals, and given reasonable pop-
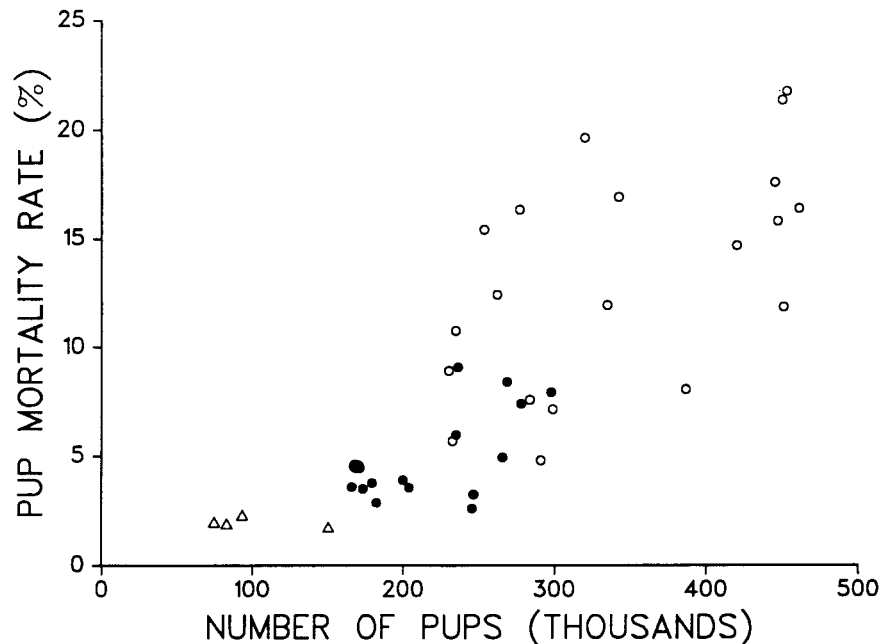
Figure 4.   Mortality rate of northern fur seal pups as a function of number of pups born on St. Paul Island, Alaska, for various years within three time periods: 1914–22 (△), 1950–70 (O), and 1972–87 (●). Data are from Lander (1980), York (1985), and, for recent years, unpublished records at the National Marine Mammal Laboratory, Seattle.

ulation growth rates, it appears that a minimum of about 10 annual population indices are required (Boveng *et al.* 1988, Gerrodette 1988). Further study of the statistical power of dynamic response analysis with both simulated and actual data is needed, particularly, as with the California gray whale, when the population growth rate is low and curvature is barely detectable.

On the other hand, a back-calculation analysis does not require a time series of population size estimates. It does require an estimate of current population size, estimates of past birth and death rates of the population, again augmented by data on incidental kills or harvest, and knowledge of where MNPL falls as a fraction of carrying capacity. Data requirements are greater than for dynamic response, and the data are not used as efficiently to answer the specific management question at hand (Goodman 1988). Partly because of difficulties in applying this technique to determine OSP for eastern tropical Pacific dolphin populations, the MMPA was amended in 1984 to authorize the taking of certain dolphin populations without having to make an OSP determination (Marine Mammal Commission 1986).

Different methods of OSP determination may also be contrasted by the meaning attached to carrying capacity. Whether current or historical carrying capacity is to be used when making an OSP determination is presently an unresolved issue in marine mammal management. To allow carrying capacity

(as used in an OSP determination) to be reduced when habitat is lost is contrary to the spirit of the MMPA, but the acceptance of historical carrying capacity as the standard in all cases is also unreasonable. When reversible changes have taken place in the habitat, efforts should be made to restore the "health and stability" of the ecosystem. But some changes have been made that, for all practical purposes, are irreversible. In such cases, we must have some way of making an OSP determination in relation to current carrying capacity, even though the population has never been observed at that level.

Back calculation is, by definition, an attempt to estimate historical carrying capacity. However, carrying capacity could also be measured in current terms, by available food for example. A complicating factor in this case is that prey abundance may change with time, and if prey species also are harvested, the amount of fishing may have a substantial impact on the estimated carrying capacity. Dynamic response analysis measures OSP status in current terms when used with the most recent sequence of population estimates, but it could also be used to measure historical carrying capacity when used with a sequence of past population estimates. The analysis gives an estimate of OSP status pertaining to the time spanned by the sequence of population estimates.

Relative OSP measures that do not require a population's MNPL to be estimated have several advantages over those that do. However, such OSP measures must have certain practical and theoretical characteristics. They must be easily measured, highly consistent, sufficiently detectable and have a theoretically derivable critical value indicating whether a population with such a value is above or below its MNPL. Because of the need to derive a critical value theoretically, the outlook for developing a quantitative OSP measure from the criteria of Eberhardt and Siniff (1977) or the general regulatory model of Eberhardt (1977) is doubtful. Dynamic response analysis may succeed because what it uses as a critical value, a change from accelerating to decelerating population growth, is the *definition* of MNPL. To rest on as solid a theoretical foundation, any other OSP measure developed in the future will similarly have to use as its metric a quantity that is part of the definition of MNPL.

Marine mammal monitoring programs usually try to estimate the size of some accessible portion of the population. While such information can at least indicate trends in population size, and dynamic response analysis was developed in response to such data-poor situations, we need other kinds of information to improve management of marine mammal populations. For one thing, the inevitable errors associated with estimating an abundance index mean that data must be collected over a number of years before a trend is statistically significant. Although the number of years required to detect a trend can be estimated (Gerrodette 1987), the trend can be detected only after it has happened. For long-lived, slowly reproducing animals such as marine mammals, this is usually too late for effective management. The result may be a succession of "crisis" responses. Fay *et al.* (1989) showed how inadequate monitoring and poor communication have caused the Pacific walrus (*Odobenus rosmarus*) to fluctuate through three wide cycles in population size over the last 150 yr. Monitoring a population condition index in addition to an abundance index has the potential

to detect demographic changes at an earlier stage and also provides a comple-
mentary type of information useful in management (Table 1).

If our assessment of the current situation is correct, it would be worthwhile
to develop more approaches to making quantitative OSP determinations. As
noted earlier, any consideration of new approaches must keep in mind the type
of data that can be collected for marine mammal populations. One possible
new approach is to explore ways of combining several qualitative but independent
measures of population status. It is also important to remember that all of this
discussion has taken place within the framework of the current single-species
definition of OSP. A more long-term solution is to develop the theoretical and
practical tools for true ecosystem management. Assessment of the data necessary
to make informed management decisions in the controversial area of the impact
of seals on fisheries is a first step toward this goal (Beddington *et al.* 1985,
Gulland 1987, Harwood and Croxall 1988).

LITERATURE CITED

ALLEN, K. R. 1976. A more flexible model for baleen whale populations. Reports of
    the International Whaling Commission 26:247–263.
BEAN, M. J. 1983. The evolution of national wildlife law. Praeger Scientific, Urbana,
    IL. 448 pp.
BEDDINGTON, J. R., R. J. H. BEVERTON AND D. M. LAVIGNE, eds. 1985. Marine mammals
    and fisheries. George Allen & Unwin, London. 354 pp.
BOVENG, P., D. P. DeMASTER AND B. S. STEWART. 1988. Dynamic response analysis.
    III. A consistency filter and application to four northern elephant seal colonies.
    Marine Mammal Science 4:210–222.
BREIWICK, J. M., E. D. MITCHELL AND D. G. CHAPMAN. 1981. Estimated initial
    population size of the Bering Sea stock of bowhead whale, *Balaena mysticetus*: an
    iterative method. Fishery Bulletin (U.S.) 78:843–853.
BREIWICK, J. M., L. L. EBERHARDT AND H. W. BRAHAM. 1984. Population dynamics
    of western Arctic bowhead whales (*Balaena mysticetus*). Canadian Journal of Fisheries
    and Aquatic Sciences 41:484–496.
COOKE, J. G. 1986. On the net recruitment rate of gray whales with reference to inter-
    specific comparisons. Reports of the International Whaling Commission 36:363–
    366.
DeMASTER, D. P. 1981. Incorporation of density dependence and harvest into a general
    population model for seals. Pages 389–401 *in* C. W. Fowler and T. D. Smith, eds.
    Dynamics of large mammal populations. John Wiley & Sons, New York, NY.
DeMASTER, D. P. 1984. A review of density dependence in marine mammals. Pro-
    ceedings of the Workshop on Biological Interactions among Marine Mammals and
    Commercial Fisheries in the Southeastern Bering Sea. Alaska Sea Grant Report 84-
    1, pp. 139–148.
DeMASTER, D. P., D. J. MILLER, D. GOODMAN, R. L. DeLONG AND B. S. STEWART. 1982.

Assessment of California sea lion fishery interactions. Transactions of the 47th North American Wildlife and Natural Resources Conference, Wildlife Management Institute, Washington, D.C. pp. 253–264.

EBERHARDT, L. L. 1977. Optimal policies for conservation of large mammals, with special reference to marine ecosystems. Environmental Conservation 4:205–212.

EBERHARDT, L. L., D. G. CHAPMAN AND J. R. GILBERT. 1979. A review of marine mammal census methods. Wildlife Monographs 63, 46 pp.

EBERHARDT, L. L., AND D. B. SINIFF. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34:183–190.

ESTES, J. A., AND J. F. PALMISANO. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058–1060.

FAY, F. H., B. P. KELLY AND J. L. SEASE. 1989. Managing the exploitation of Pacific walruses: a tragedy of delayed response and poor communication. Marine Mammal Science 5:1–16.

FOWLER, C. W. 1981. Density dependence as related to life history strategy. Ecology 62:602–610.

FOWLER, C. W. 1984. Density dependence in cetacean populations. Pages 373–379 in W. F. Perrin, R. L. Brownell, Jr. and D. P. DeMaster, eds. Reproduction in whales, dolphins and porpoises. Reports of the International Whaling Commission, Special Issue 6.

FOWLER, C. W. 1988. Population dynamics as related to rate of increase per generation. Evolutionary Ecology 2:197–204.

GERRODETTE, T. 1987. A power analysis for detecting trends. Ecology 68:1364–1372.

GERRODETTE, T. 1988. Dynamic response analysis. II. Evaluation of dynamic response analysis in a simulated no-harvest case. Marine Mammal Science 4:196–209.

GILPIN, M. E., T. J. CASE AND F. J. AYALA. 1976. θ-selection. Mathematical Biosciences 32:131–139.

GOODMAN, D. 1988. Dynamic response analysis. I. Qualitative estimation of stock status relative to maximum net productivity level from observed dynamics. Marine Mammal Science 4:183–195.

GULLAND, J. A. 1987. Seals and fisheries: a case for predator control? Trends in Ecology and Evolution 2:102–104.

HARWOOD, J., AND J. P. CROXALL. 1988. The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. Marine Mammal Science 4:13–33.

HOLT, S. J., AND L. M. TALBOT. 1978. New principles for the conservation of wild living resources. Wildlife Monographs 59, 33 pp.

KENYON, K. W. 1969. The sea otter in the eastern Pacific Ocean. U.S. Fish and Wildlife Service, North American Fauna 68. [Also Dover Publications, New York, NY, 1975, 352 pp.]

LANDER, R. H., ed. 1980. Summary of northern fur seal data and collection procedures. NOAA Technical Memorandum NMFS-F/NWC-3, 162 pp.

LANKESTER, K., AND J. R. BEDDINGTON. 1986. An age structured population model applied to the gray whale (Eschrichtius robustus). Reports of the International Whaling Commission 36:353–358.

MARINE MAMMAL COMMISSION. 1986. Annual report of the Marine Mammal Commission, calendar year 1985. A report to Congress. Marine Mammal Commission, Washington, D.C., 180 pp.

OHSUMI, S. 1976. Population assessment of the California gray whale. Reports of the International Whaling Commission 26:350–359.

REILLY, S. B. 1981. Population assessment and population dynamics of the California gray whale (Eschrichtius robustus). Ph.D. thesis, University of Washington, Seattle, WA. 279 pp.

REILLY, S. B., D. W. RICE AND A. A. WOLMAN. 1983. Population assessment of the

gray whale, *Eschrichtius robustus*, from California shore censuses, 1967–80. Fishery Bulletin (U.S.) 81:267–279.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191:1–382.

SMITH, T. D. 1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fishery Bulletin (U.S.) 81:1–13.

SMITH, T. D., AND T. POLACHECK. 1979. Analysis of a simple model for estimating historical population sizes. Fishery Bulletin (U.S.) 76:771–779.

YORK, A. E. 1985. Estimation of numbers of pups born on St. Paul Island during 1977 and 1978. Pages 16–18 *in* P. Kozloff, ed. Fur seal investigations, 1982. NOAA Technical Memorandum NMFS-F/NWC-71.