

DEFINING "POPULATION" TO MEET MANAGEMENT OBJECTIVES FOR MARINE MAMMALS

BARBARA L. TAYLOR

Southwest Fisheries Science Center,
P. O. Box 271,
La Jolla, California 92038-0271, U.S.A.

ABSTRACT

The 1994 amendments to the Marine Mammal Protection Act (MMPA) stipulate the number of animals that may be removed from a population by human-caused mortality. One factor used for calculating this number is an estimate of minimum abundance. The minimum abundance estimate must be for a defined population unit. The definition of a population remains elusive, yet is critical to good management. This paper explores a definition of population that attempts to meet the MMPA management objectives of (1) maintaining populations at their optimum sustainable population level and (2) maintaining populations as functioning parts of their ecosystem. A model is created wherein two populations are connected by dispersal. The populations are managed as one unit, and minimum abundance is based on the combined size of the two populations. Animals are harvested from only one of the populations. Several models of dispersal are explored. For all models, when dispersal falls below a few percent per year, recruitment into the harvested population is insufficient to compensate for removal, and population levels decline below those sought by management objectives. Therefore, the two populations should be managed separately if dispersal between them is less than several percent per year. The exact percentage depends on the relative population sizes and the recovery factor, another parameter used in calculating the maximum number that may be removed. The recovery factor provides a margin of safety, which, if set conservatively, allows management objectives to be met despite uncertainty about population structure. As currently used, however, the process of setting the recovery factor ignores uncertainty in population structure.

I begin by reviewing the portions of the Marine Mammal Protection Act (MMPA) that pertain to management objectives, because these objectives determine how much populations are allowed to be reduced. The act specifies that endangered or depleted species "and population stocks should not be permitted to diminish beyond the point at which they cease to be a significant functioning element in the ecosystem of which they are a part, and consistent with this major objective, they should not be permitted to diminish below

their optimum sustainable population" It further states that "the primary objective of their management should be to maintain the health and stability of the marine ecosystem. Whenever consistent with this primary objective, it should be the goal to obtain an optimum and sustainable population keeping in mind the carrying capacity of the habitat."

As guidance to interpreting these management objectives, the act defines "optimum sustainable population" (OSP) as: "with respect to any population stock, the number of animals which will result in the maximum productivity of the population or the species, keeping in mind the carrying capacity of the habitat and the health of the ecosystem of which they form a constituent element." By regulation, the National Marine Fisheries Service defined populations to be at OSP when they were between carrying capacity (K) and the maximum net productivity level (MNPL; Gerrodette and DeMaster 1990).

Furthermore, the act defines "population stock" as "a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature." This paper emphasizes the importance of defining appropriate population units to calculate the number of animals that can be removed from populations to meet both the population and ecosystem management objectives of the act.

The 1994 amendments to the act allow regulation of human-caused mortality through the calculation of potential biological removals (PBRs). One element of the equation used to calculate PBR is an estimate of abundance. Presumably, this estimate is made for each population stock. Use of the term *population stock* implies that both a biological (population) and a management (stock) meaning are intended. For brevity, I use "population" instead of "population stock" to carry the same double meaning: (1) groups that are delineated by a low rate of genetic exchange, or (2) groups of animals that are defined by elevated risk and thus are managed separately. These meanings are often referred to by separate names, the former being called an evolutionary significant unit and the latter, a management unit.

Populations are defined as evolutionary significant units as a means of preserving the genetic diversity of the species (Waples 1991). Dizon *et al.* (1992) offer a phylogeographic approach that categorizes stocks as to their probability of being an evolutionary significant unit, a unit used under the Endangered Species Act. Moritz (1994) regards stocks to be synonymous with management units and argues that they are the logical unit for short-term management. Perrin and Brownell (1994) contend that "stock" identity cannot be divorced from the management strategy adopted. There is no doubt that population units which are significant in an evolutionary sense qualify as population stocks under the MMPA. However, preserving only evolutionary significant units could allow reduction and/or fragmentation of present ranges and thus violate the ecosystem goals of the MMPA.

As an example, consider the schematic distributions in Figure 1. Distribution a is the pristine distribution where width represents abundance and length represents geographic distance. Constrictions in this schematic represent a barrier to movement such that this distribution could be described as

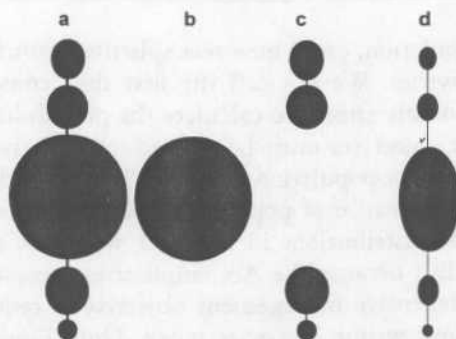


Figure 1. Distribution of pristine populations (a), versus potential distributions after 50% of the total abundance is removed (b-d). Width represents abundance; length represents distance.

a series of populations connected by dispersal (the aggregate is often called a metapopulation). If we reduced abundance by 50%, we could obtain any of the other distributions: b, range contraction; c, range fragmentation; or d, range maintenance. Although all may meet the population goal of maintaining populations within OSP—*i.e.*, above about 50% of K —b and c probably do not meet the ecosystem goal. But because there are no population-definition "rules" for calculating PBRs, any of these alternatives could occur, depending on the distribution of human-caused mortality.

The Act's definition of population stock provides little guidance. Unfortunately, managers have found it impossible to use the criterion "interbreed when mature" for most species. If we interpret "interbreed when mature" to represent the degree of genetic interchange, then nature presents us with a continuum. Some geographically separate groups of animals may exchange members at the rate of one per generation; others may exchange at the rate of one percent per year. If we restrict our definition of population stock to only those virtually closed populations exchanging individuals at the rate of a few individuals per generation, then we will only have population boundaries encircling large geographic ranges. These ranges may be composed of disparate habitats. Calculating the PBR from abundance estimates for these units may allow depletion of areas with large human-caused mortalities, *i.e.*, result in distributions b and c.

Irrespective of difficulties defining populations, the National Marine Fisheries Service must draw lines on a map to represent population boundaries, and must do it for the 48 marine mammal species that inhabit U.S. waters. Information on which to base such decisions about population boundaries ranges from very crude distributional data to very detailed data on movement, morphology, genetics, and distribution. Most of the time, however, to meet the Act's management objectives, the implementing agency must make decisions in the face of considerable uncertainty.

Two types of errors can be made in making these decisions: (1) incorrect lumping of populations, which could result in not reaching MNPL or even

eliminating one population, or (2) incorrect splitting, which may unnecessarily restrict human activities. We can call the first the "conservation error" and the second the "economic error." To calculate the probabilities of making these errors, management objectives must be defined quantitatively. For purposes of illustration, I assume that population growth is logistic and thus MNPL occurs at 50% of K . If maintenance of populations above 50% of K were the only objective, any of the distributions in Figure 1 would be an acceptable management outcome. But because the Act emphasizes ecosystem integrity, I believe a more comprehensive management objective is required, *i.e.*, one that considers distributions within a species range. Only Figure 1d would be an acceptable outcome if management objectives are to both maintain populations above MNPL and maintain an unfragmented and undiminished range.

For purposes of this paper, I reduce this problem to two populations, and model a worst-case scenario where two populations connected by dispersal are managed as a single unit even though human-caused mortality occurs in only one population. This exercise demonstrates the importance of management objectives in defining populations, how dispersal rates below a threshold value result in loss of the harvested population, and how uncertainty about population structure can be included in the calculation of allowable levels of mortality.

METHODS

Using only two populations to illustrate how dispersal affects management options simplifies the interpretation of results. Although this model is a simplified worst-case scenario, it is not dissimilar to the management problem of central and northern California harbor porpoises (*Phocoena phocoena*; Barlow and Forney 1994), considered as an example in the discussion. For this model, I assume that both hypothetical populations are managed as a single unit and that both experience logistic growth:

$$N_{t+1} = N_t + rN_t \left(1 - \frac{N_t}{K}\right) \quad (1)$$

where N = population size,
 t = time,
 r = maximum intrinsic rate of growth, and
 K = carrying capacity (historical abundance).

The maximum number of animals that can be removed from a population is called the PBR:

$$PBR = N_{MIN} r_{MNPL} F_R \quad (2)$$

where PBR = potential biological removal,
 N_{MIN} = a population estimate that is probably exceeded by the true population size,
 r_{MNPL} = growth rate at maximum net productivity, and
 F_R = a recovery factor.

Default values for some parameters were proposed in Wade (1998) and have been accepted for use in calculating PBRs: $r_{MAX} = 0.04$, cetaceans; $r_{MAX} = 0.12$, pinnipeds; $r_{MNPL} = r_{MAX}/2$; N_{MIN} = the lower 20th percentile of the distribution for the abundance estimate, and $F_R = 0.50$. Data can be uncertain by being imprecise and/or biased.

For an intuitive grasp of the PBR management scheme, let me make an analogy to shooting at a target. Instead of a bullseye, the target is a square with a horizontal line bisecting the midpoint. For any given shot at the target, the goal is to always (*i.e.*, with high probability) place your round above the line. This symbolizes maintaining populations above MNPL. Imagine that you want to make certain when you shoot that you hit above this line 95% of the time. Now consider two guns: a pilgrim's musket and a sniper's rifle. The rifle shoots with great precision and is equivalent to an abundance estimate with a very low coefficient of variation (CV). Even an expert marksman, however, would be considerably less precise with the musket; repeated attempts with the musket produce a more diffuse pattern than with the rifle. In order to insure a high chance of hitting the target above the line, the marksman would deliberately aim the musket higher than the rifle. Using N_{MIN} in the PBR equation effectively raises the aiming point to adjust for poorer precision. How high above the line the marksman needed to aim was decided by simulating marine mammal management. The simulations both estimated abundance and removed the estimated PBR from model populations. Using the lower 20th percentile of the distribution of abundance estimates assured that populations equilibrated within OSP in 95% of the simulations. In other words, the marksman placed his or her round above the line 95% of the time.

The second important consideration for a marksman is whether firearms have been correctly sighted. If the sights are improperly adjusted, the marksman may aim above the line but consistently hit below it. The amount that the shot is consistently off the mark is called bias in statistical terms. We may photograph seals and get very repeatable (precise) counts but miss a proportion that are at sea. Therefore, a second set of simulations was used to examine bias in the estimated parameters. In risk-averse management, overestimation of PBR poses a risk to populations; underestimation does not. For example, one scenario overestimated the abundance by a factor of two. Such an overestimate could come from the relatively unlikely event of animals being attracted to the survey vessel or, more likely, from animals being included in the abundance estimate that were really part of another population. The possibility of such errors led to the setting of default values for the recovery factor (F_R) such that 95% of the simulated populations equilibrated within OSP despite such errors. If the possible factors that cause bias are eliminated, this parameter can be raised to a value of one. Doing so, however, dramatically reduces the safety margin for managing the species.

How different levels of uncertainty affect equilibrating population sizes is shown in Figure 2a. Without bias in the abundance estimate, mean population levels will equilibrate according to:

$$\frac{N}{K} = 1 - \frac{mF_R}{2} \quad (3)$$

The parameter m is the fraction of the mean abundance estimate used for N_{MIN} ($N_{MIN} = mN_{MEAN}$). This fraction can be calculated for a log-normal distribution from equation 4:

$$m = e^{z\sqrt{\ln(1 + CV^2)}} \quad (4)$$

where Z = desired percentile from the Z -distribution, and
 CV = coefficient of variation of the abundance estimate.

For the lower 20th percentile of the distribution of abundance estimates, $Z = -0.842$. To understand these equations, consider the case where abundance is known exactly, *i.e.*, $CV = 0$ and $F_R = 1$. Solving equations 3 and 4 yields $N/K = 0.5$, which is MNPL. In this case, the PBR equals the productivity at MNPL. Note that because $CV = 0$, the lower 20th percentile of the distribution, which consists of a spike with a probability of one at the mean abundance estimate, is the abundance estimate itself and therefore m , the proportion of the mean estimate used for N_{MIN} , is one. If we use a CV typical of marine mammals, $CV = 0.3$, solving equation 4 yields $m = 0.781$. Thus, to keep the population above MNPL 95% of the time, we are now aiming at $N/K = 0.609$ (see Fig. 2a with $F_R = 1$). As CV s increase, the distributions for abundance estimates widen and the lower 20th percentile of the distribution (N_{MIN}) becomes an increasingly small proportion of the mean abundance estimate. If we do not know whether our data are biased and use the default of $F_R = 0.5$, then our target becomes $N/K = 0.805$. The more uncertain our data, as reflected by high CV s or low recovery factors, the more conservative the management.

The difference between MNPL (symbolized by the dashed line in Fig. 2a) and the equilibrium population sizes (N/K , the solid lines in Fig. 2a) is the margin of error allowed for the level of uncertainty about the true state of the population. This margin of error provides a margin of safety from incorrect population designations. The proportion of a cetacean population that is allowed to be removed at the equilibrium levels in Figure 2a is shown in Figure 2b. At MNPL ($N/K = 0.5$), the growth rate (r) is 0.02, and the proportion of the population removed (PBR/N) is also 0.02 when knowledge is perfect ($CV = 0$, $F_R = 1$). For an endangered species ($F_R = 0.1$), even if $CV = 0$, only one-tenth of the productivity at MNPL is allowed to be removed, and the population equilibrates at 95% of K . (Note that for logistic growth $r = r_{MAX} - (N/K) \times r_{MAX}$, so when $N/K = 0.95$ we have $r = 0.04 - 0.95 \times 0.04 = 0.002$.)

Dispersal is represented in three alternative models that increase in complexity. The first model assumes that each individual has a fixed probability of dispersing (D). If $D = 0.01$ then any individual has a 1% chance of dispersing. The second model assumes that the probability of dispersing depends on the density of animals in the "home" population:

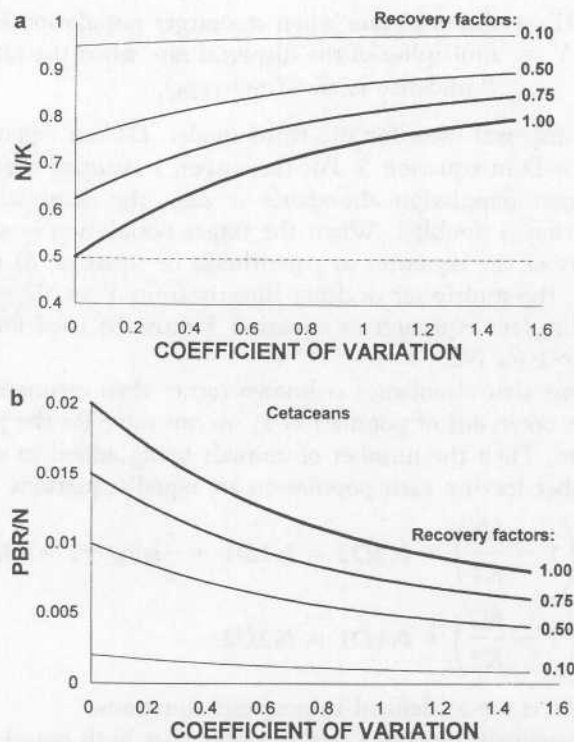


Figure 2. Equilibrium population levels for different CVs and recovery factors (a). PBRs with respect to K are shown for cetaceans (b), but would be three times these levels for pinnipeds. Note that reducing F_R from 1.0 to 0.5 reduces PBR/K by a constant amount so that the percent reduction increases with increasing CVs (decreasing precision).

$$D1 = D \frac{N1}{K1} \quad (5)$$

where $D1$ = dispersal rate for population 1,
 D = maximum dispersal rate,
 $N1$ = abundance for population 1, and
 $K1$ = carrying capacity for population 1.

Population 2 would have an equivalent equation. The maximum dispersal rate (D) is achieved at K , which assumes that individuals are most likely to disperse when their populations have reached whatever level limits their growth to zero. The third model assumes that dispersal is influenced not only by the density of the home population but also by the density of the "target" population. The density of the target population can be accounted for by making D a function of the density of the target population:

$$D1' = D1 \left(Y - \frac{Y-1}{K2} N2 \right) \quad (6)$$

where $D1'$ = maximum dispersal rate (in this case for population 1),

$D1$ = dispersal rate when the target population is at K , and
 Y = multiplier of the dispersal rate when the target population abundance is zero (intercept).

To calculate dispersal rates for the third model, $D1'$ in equation 6 must be substituted for D in equation 5. For this paper, I assumed that $Y = 2$. Thus, when the target population abundance is zero, the dispersal rate from the home population is doubled. When the target population is at K , the multiplier (the part of the equation in parentheses in equation 6) is 1 and $D1 = D$. Therefore, the multiplier declines linearly from Y at $N2 = 0$ to 1 at $N2 = K$. An equivalent equation to equation 5 must be used for population 2, substituting $N1$ for $N2$.

If we assume that abundance is known rather than estimated and that the entire PBR is taken out of population 1, we can solve for the population sizes at equilibrium. Then the number of animals being added to each population and the number leaving each population are equal (equations 7 and 8):

$$rN1\left(1 - \frac{N1}{K1}\right) + N2D2 = N1D1 + \frac{r}{2}mF_R(N1 + N2), \text{ and} \quad (7)$$

$$rN2\left(1 - \frac{N2}{K2}\right) + N1D1 = N2D2. \quad (8)$$

where parameters are as defined in previous equations.

If the management objective requires only that both populations be maintained above MNPL, then we want sufficient dispersal to maintain at a minimum $(N1 + N2)/(K1 + K2) = 0.5$. If we let this proportion of the aggregate K be symbolized by P , we can solve for the equilibrial population sizes of each population. The equations below apply to model 1:

$$\frac{N2}{K2} = \frac{-b + \sqrt{b^2 - 4ac}}{2a} \quad (9)$$

where the parameters for the quadratic equation are

$$a = -\frac{K2}{K1} - 1, \quad b = \frac{2J}{K1}, \quad c = \frac{J}{K2}\left(1 - \frac{F_R m}{2} - \frac{J}{K1}\right),$$

$$J = P(K1 + K2), \quad \frac{N1}{K1} = J - N2, \text{ and} \quad (10)$$

$$D = \frac{rN2\left(1 - \frac{N2}{K2}\right)}{N2 - N1}. \quad (11)$$

These equations must also satisfy the conditions that neither population can exceed K or be negative, and the dispersal rate cannot be negative.

A second set of equations is needed for the management objective that requires both that the aggregate population be kept above MNPL, and that

the harvested population never be allowed to fall below a threshold value. It may be desired that this value be some fraction of its K ($X = N1/K1$). Therefore, if equation 10 falls below X , the following parameters are used in equation 9:

$$a = -1, \quad b = 1 - \frac{F_R m}{2}, \quad \text{and} \quad c = \frac{XK1}{K2}(1 - X - F_R m).$$

The equilibrium abundance for $N1$ becomes

$$N1 = \frac{N2 \left(\frac{F_R m}{2} - 1 + \frac{N2}{K2} \right)}{1 - X - \frac{F_R m}{2}}. \quad (12)$$

RESULTS

Figure 3 shows the equilibrium population sizes with respect to K for different dispersal rates. When $K1 = K2$, the default values are used in calculating PBR, and the coefficient of variation in the abundance estimate (CV) = 0.3. The middle curve in the figures represents P , the proportion of the aggregate population. Stable equilibrium is shown in bold. When dispersal rates decline below the point where the curve doubles back on itself (and goes from unstable to stable), population 1 goes extinct. Below this level, the equilibrium $N2$ is

$$N2 = K2 \left(1 - \frac{D}{r} \right). \quad (13)$$

Because $N1 = 0$, the aggregate population level is $N2/(K1 + K2)$. The reason for this abrupt change in behavior relates to properties of exponential growth. In essence, below a threshold dispersal rate, recruitment is less than removal, which means that the effective r in equation 1 is < 0 . If $r < 0$, then the population *will* go extinct with the rate depending on the magnitude of r . Similarly, if $r > 0$ then the population *will* grow. As r becomes arbitrarily small, the time to reach an equilibrium becomes arbitrarily long. $N1/K1$ at this threshold dispersal rate could be one definition of the threshold value needed to maintain a species throughout its range.

The threshold dispersal rate needed for $N1/K1 > 0$ is shown for different F_{RS} and CVs (Fig. 4). The point at which $(N1 + N2)/(K1 + K2) = 0.5$ is at a threshold dispersal rate of about 1% per year when $K1 = K2$ for cetaceans. For pinnipeds, it is three times this value because their growth rate is three times higher. The corresponding F_{RS} for CVs of 0.1, 0.3, and 0.5 are 0.67, 0.71, and 0.80. If F_R is set higher than these values, then the aggregate population will not reach $0.5K$, and this management objective will not be met. Note that it is not possible, given these CVs, to meet the management

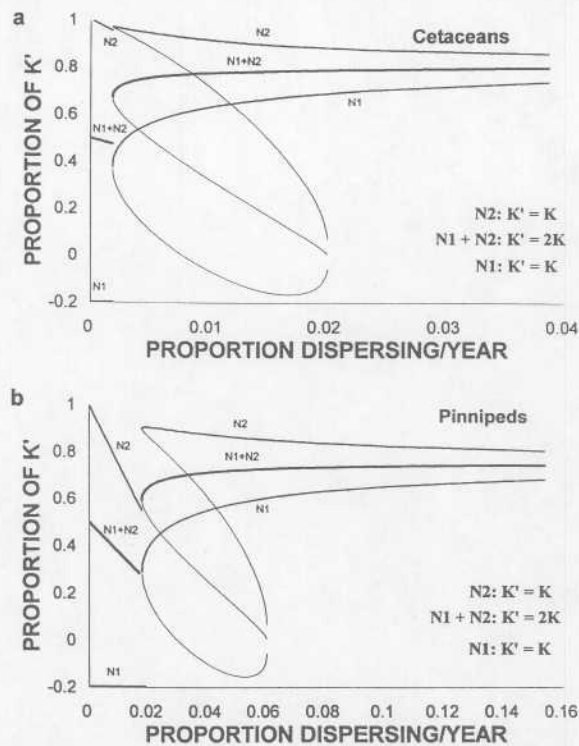


Figure 3. The equilibrium proportion of K reached for $N2$ (top curves), $N1$ (bottom curves), and $N1 + N2$ (middle curves in bold) versus the constant D for model 1. Stable equilibrium is shown in bold. $N1$ goes extinct below a threshold dispersal rate—0.002 for cetaceans (a), 0.02 for pinnipeds (b).

objective if $F_R = 1$. The margin of error given by these CVs is not sufficient to overcome the incorrect lumping of populations. We can solve equation 9 for $(N1 + N2)/(K1 + K2) = 0.5$ for different CVs and F_R s (Fig. 5). For pinnipeds, which often have CVs < 0.2 , the dispersal rate needed to overcome incorrect lumping increases dramatically as F_R is increased. For the case shown ($K1 = K2$), if $F_R = 0.9$ and $CV = 0.1$, a dispersal rate of 6% per year would be needed to maintain the aggregate population at MNPL. It is extremely unlikely that such a high dispersal rate could be detected with genetic data. To detect such a dispersal rate would probably require dispersal data acquired by following individuals (photographic identification, tagging, or branding).

The situation becomes more complex when the adjacent populations differ in abundance. Figure 6 shows the threshold dispersal rates and equilibrium population levels for those dispersal rates for a range of $K1/K2$ ratios ($CV = 0.3$, $F_R = 0.5$). With these levels of uncertainty, no dispersal is required to maintain $N1$ when it is $> 1.2 \times N2$. As before, results are highly influenced by F_R (Fig. 7). Given the default of $F_R = 0.5$, the objective of maintaining the aggregate population $> 0.5K$ is always met at the threshold dispersal rate. As F_R increases, this aggregate level is quickly reduced to levels $< 0.5K$.

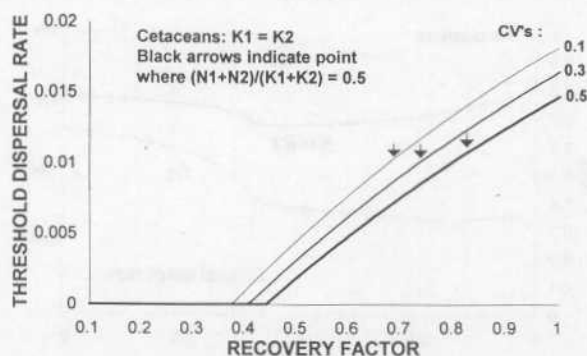


Figure 4. The threshold dispersal rate needed to keep N_1 extant for different recovery factors and CVs of 0.1, 0.3, and 0.5. Arrows are shown for a possible management objective to maintain the aggregate population of at least MNPL: $(N_1 + N_2)/(K_1 + K_2) = 0.5$. Recovery factors greater than the value indicated by the arrows would fail to meet this objective; those less than this value would meet the objective. For example, if $F_R = 1$, the objective could not be met for any of the CVs shown if the threshold dispersal rate was used as the criterion to determine whether or not to lump the populations. Threshold dispersal rates for pinnipeds are three times the values shown here for cetaceans.

Figure 7b shows that N_1/K_1 remains fairly constant over large ranges of K_1/K_2 . When $F_R = 1$, N_1/K_1 remains at about 0.075. It could be questioned whether this level meets the definition of maintaining populations as significant functioning elements of their ecosystems. It is in this range that a different threshold value may be considered as a management objective.

The threshold dispersal rate is reduced for models 2 and 3 (Fig. 8). Most of the reduction is a result of density-dependent dispersal in the home pop-

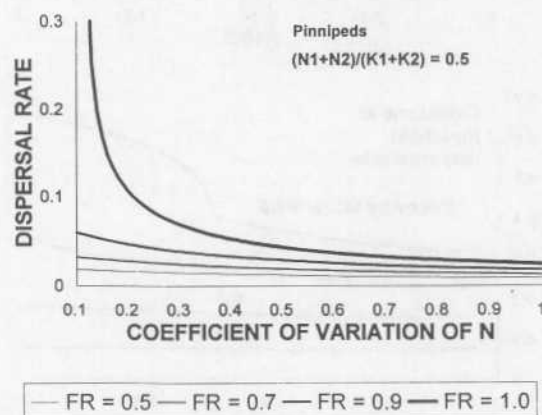


Figure 5. The dispersal rate required to maintain 50% of the aggregate population for different CVs and F_R s when $K_1 = K_2$. The curves represent the analytical solution to demonstrate the effect of changing the parameters that incorporate uncertainty. The reader should be aware, however, that some of the points shown are for unstable equilibria.

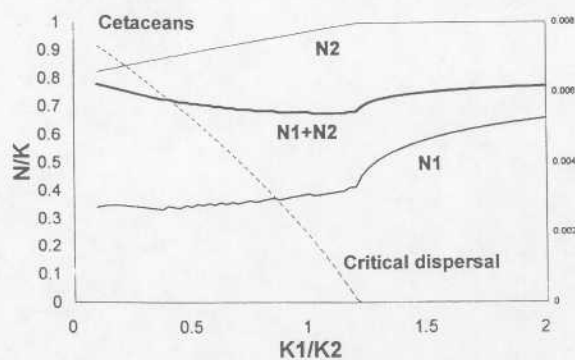


Figure 6. Equilibrium population levels at the threshold dispersal rate for different ratios of $K1/K2$ with $CV = 0.3$. Threshold dispersal is given by the second Y-axis. Threshold dispersal rates for pinnipeds are three times the values shown here for cetaceans.

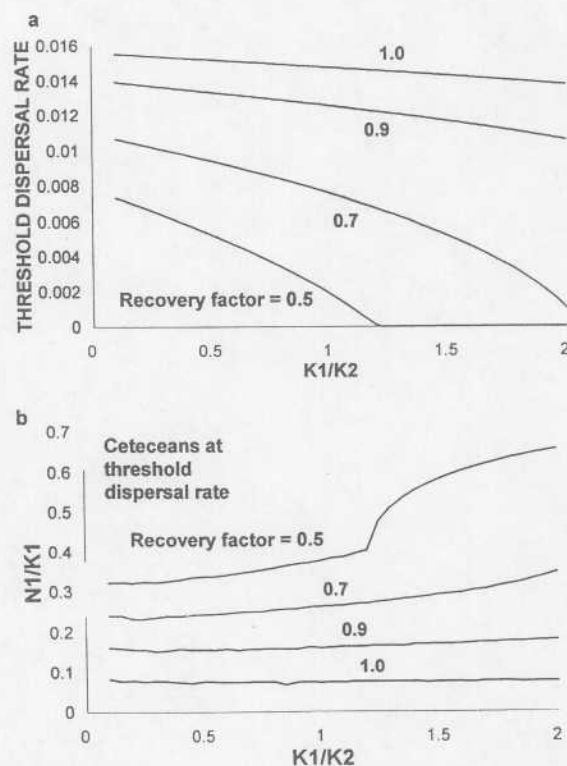


Figure 7. Threshold dispersal rates (a), and equilibrium population levels at threshold dispersal rates (b) for different ratios of $K1$ to $K2$ and for different recovery factors. When $F_R < 0.7$, the objective of $(N1 + N2)/(K1 + K2) \geq 0.5$ is always met, and $N1$ is always at greater than 20% of $K1$. In contrast, when $F_R = 1$, this objective is met only when $K1/K2 < 0.2$, and $N1/K1$ remains at levels close to 0.075.

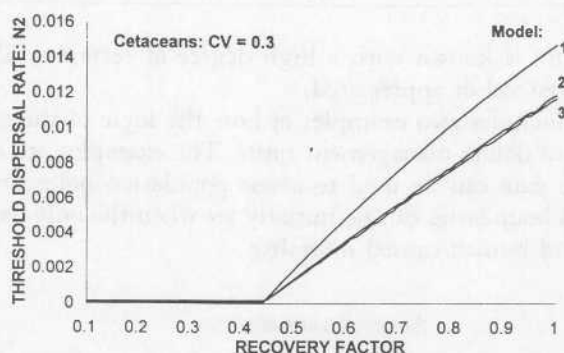


Figure 8. Threshold dispersal rates for N_2 for the three models of dispersal for cetaceans with $K_1 = K_2$, $CV = 0.3$ for different recovery factors.

ulation (model 2). Adding dispersal that is also dependent on the density of the target population makes very little difference in the threshold dispersal rate.

DISCUSSION

Whatever the model chosen, the conclusion is the same: if dispersal rates are less than a few percent per year, then there is a danger of depleting the combined population or eliminating the harvested population if population structure is ignored and human-caused mortality is concentrated in one population. The results differ depending on the proportion of the total population represented by each population and on the amount of uncertainty incorporated via F_R and the CV.

PBRs seem relatively simple to calculate only because the sole numerical inputs are abundance estimates and default values for growth rates. This exercise with two populations demonstrates, however, that the success of the management scheme also requires knowledge of population structure. The PBR management scheme was originally tested via simulations that included the possibility that the abundance used for N_{MIN} was overestimated by a factor of two (Taylor 1993, Wade 1998). Treating the central and northern California harbor porpoise populations as a single management unit when they were not would overestimate N_{MIN} by a factor of more than three. Even if the central California harbor porpoises were eliminated, more than 50% of the harbor porpoises in California would remain. Thus, management objectives may be met if objectives were simply to maintain aggregate populations greater than MNPL without regard to range fragmentation or reduction. This points out the crucial importance of quantitatively defining management objectives.

The exercise has also demonstrated that the margin of safety provided by using low values for F_R can compensate for uncertainty in knowing population structure. Alternatively, use of $F_R = 1$ implies not only that there is no bias in estimates of abundance, mortality, and maximum growth rates, but that

population structure is known with a high degree of certainty. The latter is insufficiently understood or appreciated.

The Appendix includes two examples of how the logic of the models used here can be used to define management units. The examples are designed to show how genetic data can be used to assess population boundaries, as well as how population boundaries can be initially set when the only data available are distribution and human-caused mortality.

ACKNOWLEDGMENTS

Thanks to Andrew Dizon, Susan Chivers, Douglas DeMaster, Jay Barlow, and two very astute anonymous reviewers for reviewing this manuscript.

LITERATURE CITED

- BARLOW, J., AND K. A. FORNEY. 1994. An assessment of the 1994 status of harbor porpoise in California. National Oceanic and Atmospheric Administration. Technical Memorandum. National Marine Fisheries Service. Southwest Fisheries Science Center 205. 17 pp.
- CALAMBOKIDIS, J., AND J. BARLOW. 1991. Chlorinated hydrocarbon concentrations and their use for describing population discreteness in harbor porpoises from Washington, Oregon, and California. Pages 101–110 in J. E. Reynolds III and D. K. Odell, eds. Marine mammal strandings in the United States. NOAA Technical Report NMFS 98.
- DIZON, A. E., C. LOCKYER, W. F. PERRIN, D. P. DEMASTER, AND J. SISSON. 1992. Rethinking the stock concept: A phylogeographic approach. *Conservation Biology* 6:24–36.
- GERRODETTE, T., AND D. P. DEMASTER. 1990. Quantitative determination of optimum sustainable population level. *Marine Mammal Science* 6:1–16.
- MORITZ, C. 1994. Defining 'evolutionary significant units' for conservation. *Trends in Ecology and Evolution* 9:373–375.
- PERRIN, W. F., AND R. L. BROWNELL, JR. 1994. A brief review of stock identity in small marine cetaceans in relation to assessment of driftnet mortality in the North Pacific. Report of the International Whaling Commission (Special Issue 15):393–401.
- TAYLOR, B. L. 1993. "Best" abundance estimates and best management: Why they are not the same. National Oceanic and Atmospheric Administration. Technical Memorandum. National Marine Fisheries Service. Southwest Fisheries Science Center 188. 20 pp.
- WADE, P. R. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Marine Mammal Science* 14. (in press)
- WAPLES, R. S. 1991. Definition of "species" under the Endangered Species Act: Application to Pacific salmon. National Oceanic and Atmospheric Administration Technical Memorandum, National Marine Fisheries Service F/NWC/194, Seattle, WA. 29 pp.

APPENDIX

Examples of Setting and Evaluating Population Boundaries

Two hypothetical examples based on harbor porpoise are presented: the first assessing boundaries when genetic data are available, and the second assessing risk of setting boundaries when only data on distribution and mortality are available.

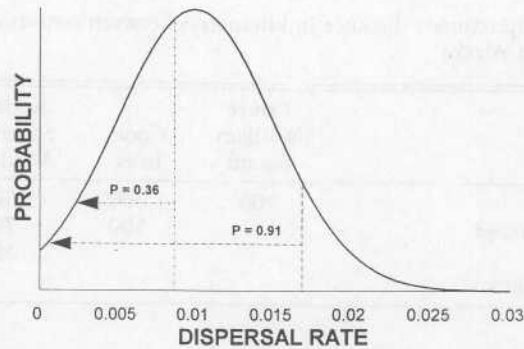


Figure A. A hypothetical probability distribution of the likelihood of different dispersal rates given genetic data. Probabilities are given for two cases: threshold dispersal when $F_R = 0.5$ (0.36) and threshold dispersal when $F_R = 1.0$ (0.91). The probabilities are the area under the curve between a dispersal rate of zero and the desired dispersal rate (such as 0.0083 for default PBR values).

The first example considers the central and northern California population designation. Central California ($N_{MIN} = 3,430$) and northern California ($N_{MIN} = 7,649$) are managed separately on the basis of pollutant data (Calambokidis and Barlow 1991). Incidental fishery mortalities occur primarily in the central California population (Barlow and Forney 1994). Because genetic data are not available for northern California, the example using genetic data for population differentiation will be hypothetical. Typically, individuals are genotyped, and population differentiation is assessed by testing the hypothesis that individuals between populations differ more than individuals from within a population. A statistic, for example Φ_{st} , is calculated to measure the degree of differentiation. Using a model about how the populations mix, we can estimate the likelihood of obtaining Φ_{st} for different dispersal rates. For example, if Φ_{st} were calculated to be 0.02, which indicates a good deal of mixing between populations, we might run our model for a high dispersal rate (such as 1% per year) and get many estimated Φ_{st} values close to our observed value. On the other hand, if we run the model for a low rate of dispersal, most estimated Φ_{st} values would be high, and we would have a very low probability of obtaining the observed Φ_{st} .

Figure A shows a hypothetical probability distribution for the likelihood that observed genetic data could result from these two populations mixing at different dispersal rates. Assume that population levels at the threshold dispersal rate meet our management objective. The threshold dispersal rate to maintain an extant population in central California if the populations are lumped and the entire PBR taken out of central California is 0.0083 (a bit less than 1% per year). Assumptions are $r = 0.04$, $F_R = 0.5$, and the ratio of current population sizes is the same as the ratio of historical population sizes ($K1/K2$). This level of dispersal maintains central California at 0.59K, northern California at 0.86K, and the aggregate at 0.77K. Examining our hypothetical probability distribution, we find that there is a 36% chance that the genetic data came from a population dispersing at a rate less than the threshold rate (the area under the curve between zero and 0.0083 is 36% of the total area). In a risk-averse policy, this one-population policy is risky, and populations should be managed separately.

Once we have a probability distribution, we can consider the effect of changing the recovery factor (F_R). Recall that F_R has a great influence on the margin of safety. When $F_R = 1$, it means that we should have no bias in the estimate of abundance, including any bias due to improper population designation. Dispersal must be 0.0166 to maintain the aggregate population at 50% of the total abundance, and population levels become 17% of K in central California and 64% of K in northern California. Looking

Table A-1. Approximate distance in kilometers between centers of areas containing harbor porpoise in Alaska.

	Prince William Sound	Cook Inlet	Kodiak, Southern Aleutians	Bristol Bay
Southeast Alaska	900	1,300	1,500	2,700
Prince William Sound		500	700	1,800
Cook Inlet			500	1,500
Kodiak, S. Aleutians				1,000

at the probability distribution, we see that our data indicate that there is a 91% chance that the dispersal rate was less than 0.0166. Thus, $F_R = 1$ leaves no doubt that using this less conservative value requires that the populations be managed separately.

Because PBRs are calculated using both N_{MIN} and F_R , the two can be traded off against each other. For example, if we lump the porpoise populations, we get a higher N_{MIN} , but because we know little about population structure we should set a low F_R . We could decide instead to split the populations and thereby reduce N_{MIN} but increase F_R because we have reduced possible bias due to incorrect population designation. We can calculate the expected PBR for different management options by multiplying the probability distribution (Fig. A) by the distribution of PBRs for those dispersal rates. Expected PBRs for some options are (1) split, $F_R = 1$, PBR = 59, (2) lump, $F_R = 0.5$, PBR = 75, and (3) lump, $F_R = 1$, PBR = 69. The reason that option 3 has a smaller expected PBR than option 2, which uses a more conservative F_R -value, is because for option 3 the harvested population goes extinct over a large range of dispersal rates. Thus, the PBR is only the number dispersing from the unharvested population for most dispersal rates, but PBRs become very high once dispersal is sufficient to maintain the harvested population. Simply calculating the expected PBR does not express the risk to the harvested population. What we do learn from this exercise is the trade-off between decisions regarding splitting or lumping and F_R level. In some situations little cost in terms of the economic error may be incurred by splitting (effectively reducing N_{MIN}) and increasing F_R (increasing the proportion of recruitment that is allowed to be removed).

The second example considers how to set initial population boundaries when few data are available. Only crude distributional data are currently available for Alaska harbor porpoise. If human-caused mortality is not evenly distributed throughout the range, defining the population as the total range is not a risk-averse strategy. Table A-1 shows the approximate distances for five geographic areas. For comparison, consider central and northern California populations, which are managed separately. The centers of these populations are approximately 500 km apart. Alaska is currently managed as a single population, and the PBR is 106. Currently there are mortality estimates for only Prince William Sound (about 20 animals/yr), and the PBR for this area alone is 29. Even if mortalities in Prince William Sound increased to five times their current level, no management action would be deemed necessary under the one population policy because the mortalities would still be less than the PBR (106). Continuing this policy at increased mortality levels could result in loss of the Prince William Sound population. Clearly, failure to meet management objectives is directly related to the amount and distribution of human-caused mortality.

To further illustrate this point, consider four different population boundary options: (1) the five-population option, where each geographic area is managed separately (Table A-1); (2) the three-population option, where Bristol Bay (which is north of the Alaska Peninsula) and Southeast Alaska are managed separately from the others, which are considered a single unit; (3) the two population option, where Bristol Bay is managed

Table A-2. Whether or not actions would be taken to reduce mortality (Yes or No) for different population options and mortality rates. If no action is taken, the threshold dispersal rate is given. D_t = threshold dispersal rate; dispersal rates less than these values would result in the extirpation of harbor porpoise in Prince William Sound.

Mortality: Prince William Sound	Management option: number of populations			
	5	3	2	1
20	No $D_t = 0.000$	No $D_t = 0.000$	No $D_t = 0.000$	No $D_t = 0.000$
40	Yes	Yes	No $D_t = 0.004$	No $D_t = 0.001$
80	Yes	Yes	Yes	No $D_t = 0.009$

separately from the others, and the others are managed as a unit; and (4) the single-population option, where all regions are managed as one population. Once the option has been chosen and the mortality is estimated, no management action is taken unless the mortality exceeds the PBRs. Table A-2 shows whether action was taken and, if not, what threshold dispersal rate would be needed to overcome an incorrect lumping decision.

Both the risk the population faces, which is a function of the amount of mortality, and what is known about dispersal for the species contribute to the decision-making process. If mortality is 20 animals, there is no difference between options. When mortality is 40, there are economic costs to fisheries under the five- and three-population options and possible conservation costs to the remaining options. We can also weight the veracity of the options because of what we know about harbor porpoise dispersal: populations only 500 km apart in California are managed separately on the basis of data from pollutant studies. The option that considers all Alaska harbor porpoise panmictic is therefore less likely than the other options. Therefore, even though the threshold dispersal rate is low, the assumption of panmixia is unlikely. Similarly, the two-population option includes Southeast Alaska, which is approximately 900 km distant and would require a threshold dispersal rate of at least 0.4% per year to keep Prince William Sound porpoise extant. When mortality reaches 80, only the single-population option requires no reduction in mortality.

This exercise demonstrates that even with no direct data, options can still be evaluated according to the risk facing the harvested population. Once boundaries have been set, scientists can gather data (genetic or about individual movement) and estimate the probability of different dispersal rates. The results of genetic analyses, however, can be interpreted only after quantitative management objectives have been specified.