A Quantitative Approach to Endangered Species Act Classification of Long-Lived Vertebrates: Application to the North Pacific Humpback Whale

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Abstract: *The U.S. Endangered Species Act (ESA) mandates that recovery plans include specific criteria to determine when a species should be removed from the List of Endangered and Threatened Wildlife. To meet this mandate, we developed a new approach to determining classification criteria for long-lived vertebrates. The key idea is that endangerment depends on two critical aspects of a population: population size and trends in population size due to intrinsic variability in population growth rates. The way to combine these features is to identify a population size and range of population growth rates (where λ denotes the annual multiplicative rate of change of a population) above which there is a negligible probability of extinction. To do so, (1) information on the current population size and its variance is specified; (2) available information on vital rates or changes in abundance over time is used to generate a probability distribution for the population's λ; (3) the lower fifth percentile value for λ (denoted as $\lambda_{(0.05)}$) is obtained from the frequency distribution of λs; and (4) if $\lambda_{(0.05)}$ is <1.0, a backwards population trajectory starting at 500 individuals for a period of 10 years is performed and the resulting population size is designated as the threshold for listing a species as endangered, or if $\lambda_{(0.05)}$ is ≥1.0, the threshold for endangerment is set at 500 animals. A similar approach can be used to determine the threshold for listing a species as threatened under the ESA. We applied this approach to North Pacific humpback whales (Megaptera novaeangliae) and used Monte Carlo simulations to produce a frequency distribution of λs for the whales under three different scenarios. Using $\lambda_{(0.05)}$, it was determined that the best estimates of current abundance for the central population of North Pacific humpback whales were larger than the estimated threshold for endangered status but less than the estimated threshold for threatened status. If accepted by the responsible management agency, this analysis would be consistent with a recommendation to downlist the central stock of humpback whales to a status of threatened, whereas the status of eastern and western stocks would remain endangered.*

Aproximación Cuantitativa a la Clasificación de Vertebrados de Vida Larga del Acta de Especies en Peligro: Aplicación a la Ballena Jorobada del Pacífico Norte

Resumen: *El acta de Especies Amenazadas de los Estados Unidos (ESA) demanda que los planes de recuperación incluyan criterios específicos para determinar cuando una especie debe ser removida de la Lista de Especies de Vida Silvestre en Peligro. Para alcanzar este mandato, desarrollamos una nueva aproximación para determinar los criterios de clasificación para vertebrados de vida larga. La idea clave es que las amenazas dependen de dos aspecto críticos de una población: tamaño poblacional y tendencias en tamaño poblacional debido a la variabilidad intrínseca de las tasas de crecimiento poblacional. La forma de combinar estas características es la identificación de un tamaño poblacional y el rango de tasas de crecimiento poblacional (donde λ denota la tasa anual multiplicativa de cambio de una población) por arriba de la cual existe una*

probabilidad de extinción neglibible. Para hacer esto 1) Se especifica la información sobre el tamaño pobla-cional actual y su varianza; 2) Se utiliza información viable sobre tasas vitales o cambios en abundancia so-bre el tiempo para generar una distribución de probabilidades para la población; 3) se obtiene el valor del percentil mas bajo para λ (denotado como $\lambda_{(0.05)}$) de la distribución de frecuencias de λs; y 4) si $\lambda_{(0.05)}$ es <1.0, se efectúa una trayectoria hacia atrás iniciando con 500 individuos por un período de 10 años y el tamaño poblacional resultante se designa como el límite para enlistar una especie bajo el estatus de en peli-gro ó si el $\lambda_{(0.05)}$ es ≥1.0, el límite para considerar amenaza se establece en 500 animales. Una aproximación similar puede ser usada para determinar los límites para enlistar especies como en peligro bajo la ESA. Apli-camos esta aproximación para la ballena jorobada del Pacífico Norte (Megaptera novaeangliae) y utilizamos simulaciones Monte Carlo para producir distribuciones de frecuencia de λs para ballenas bajo diferentes es-cenarios. Utilizando el $\lambda_{(0.05)}$, se determinó que los mejores estimadores de la abundancia actual para la po-blación central de la ballena jorobada del Pacífico Norte fueron mayores que los límites estimados para ser considerada en el estatus de en peligro, pero menor a los límites de estatus de amenazada. Si este análisis es aceptado por las agencias de manejo responsables, podría ser consistente con una recomendación de desen-listar el grupo central de ballenas jorobadas y pasarlo al estatus de amenazadas, mientras que el estatus de los grupos del Este y Oeste deberán permanecer en el estatus de en peligro.

Introduction

The U.S. Endangered Species Act (ESA) defines catego-ries for endangered and threatened species but provides no criteria for deciding when a species should be listed, delisted, or downlisted. As a result, listing and recovery actions for marine mammals, as well as other species, are widely inconsistent. The ESA was amended in 1988 to require that recovery plans include specific criteria to determine when a species should be removed from the List of Endangered and Threatened Wildlife (the list). Of the 20 marine mammal species listed under the ESA, only 7 have recovery plans. Within these plans, criteria to delist or change status (i.e., from threatened to endan-gered or vice versa) vary greatly among species. Al-though most large whale species are currently listed as endangered, the status of several populations has likely changed over the last few decades as a result of a mora-torium on commercial whaling imposed by the Interna-tional Whaling Commission (IWC). For example, the eastern North Pacific population of gray whales (*Es-chrichtius robustus*) was removed from the list in June 1994, although, due to the lack of objective classifica-tion criteria, the process was highly contentious. In re-sponse to the suggestion that a number of large whales be considered for delisting (Brownell et al. 1989), we developed a new quantitative classification scheme for making delisting or downlisting decisions and applied it to humpback whales (*Megaptera novaeangliae*) in the North Pacific.

Classification criteria, which define extinction risk, should be robust to the uncertainty associated with available data. Further, if criteria are to be useful they should be based on data that either exist or are attainable in the foreseeable future. Our approach to developing delisting or downlisting criteria for humpback whales is first to evaluate the information currently available and to identify information likely to become available. We then use this information in the context of our classifica-tion scheme. Finally we show how increasing the preci-sion of parameter estimates can improve our ability to make classification decisions.

Population Structure

Management units should be based upon the ecology and population structure of the species. For listing, delisting, and reclassifying vertebrates, the definition of species within the ESA refers to "any subspecies of fish or wildlife or plants or any distinct population segment of any species of vertebrate, fish or wildlife which inter-breeds when mature" (Endangered Species Act of 1973). Based on this definition, the U.S. Fish and Wildlife Ser-vice (USFWS) and the National Marine Fisheries Service (NMFS) developed a joint policy that includes three fac-tors to be considered in defining a potentially distinct population segment: (1) the discreteness of the popula-tion relative to the rest of the species, (2) the signifi-cance of the population segment to the species, and (3) the population segment's conservation status in relation to the ESA standard for listing, i.e., whether the popula-tion segment is endangered or threatened when treated as if it were a species (USFWS 1996).

This protocol was thought to be a useful starting point for designating management units for humpback whales in the North Pacific (for details see Gerber 1998*a*). Un-fortunately, population structure for humpback whales and other large whales is difficult to determine given (1) uncertainty in patterns of genetic diversity and the rate of exchange between putative populations, (2) the com-plexity of wintering and feeding aggregations, and (3) gaps in our basic knowledge of the species, such as un-known migratory destinations. The population structure of humpback whales appears to be linked to matrilineal

fidelity to feeding areas (Baker et al. 1987; Clapham & Mayo 1987; Katona & Beard 1990; Palsbøll et al. 1995; Calambokidis et al. 1996; Larsen et al. 1996). The persistence of such maternal traditions, as well as the fact that humpback whales return to traditional sites for reproduction, contributes to the formation and maintenance of population subdivisions among humpback whales.

One could argue that classification criteria should be based upon both individual feeding grounds and on the maintenance of breeding populations. To address this issue, we considered four approaches to designating management units: (1) one population (entire North Pacific Ocean basin); (2) three breeding subpopulations (western, central, and eastern); (3) four breeding subpopulations (western, central, eastern-mainland, and eastern-offshore); and (4) five feeding subpopulations (California-British Columbia, southeast Alaska, Prince William Sound, Kodiak, Aleutian Islands-Kamchatka). By considering all these alternative assumptions about population structure, we span the range of plausible population structures for North Pacific humpbacks.

Abundance, Trends, and Life History

Although currently we lack quantitative data on population trends for North Pacific humpback whales, there are numerous suggestions that the population is increasing (Barlow 1994; Calambokidis et al. 1997; Hill et al. 1997). Calambokidis et al. (1997) provide the most recent estimate of abundance of the North Pacific population: 5540–8000 animals, with a best estimate of 6010 (SE = 474). The minimum abundance estimates available for alternative population structure units for North Pacific humpback whales are provided by Calambokidis et al. (1997), Barlow (1994), Straley (1994), and Waite et al. (1999).

Basic life-history parameters for North Pacific humpback whales are not well known. The current sex ratio is thought to be close to parity, although it is possible that there is a male bias in the wintering grounds (Palsbøll et al. 1997). Data necessary to estimate age at sexual maturity (ASM) are not available, but it is generally thought that North Pacific humpbacks become mature between 4 and 9 years of age (Clapham & Mayo 1987; Clapham 1992; Straley et al. 1994). It is possible that ASM differs between the North Atlantic and North Pacific populations: Clapham (1992) reported that for 12 whales in the North Atlantic, the average ASM was approximately age 5, whereas Straley et al. (1994) reported an upper bound for ASM of 8 based on data from one known-aged animal in the North Pacific (Straley et al. 1994).

For North Pacific humpback whales, observations of birth intervals yield estimates of annual reproductive rates on breeding grounds at 0.58 calves per year and on feeding grounds at 0.38 calves per year (Baker et al. 1987). More recently, Straley (1994) estimated mean birth interval at 2.26 years per calf (SE = 0.13), which

without correction for sampling bias (Barlow & Clapham 1997) yields an annual reproductive rate of 0.44 calves per year. Straley (1994) used a Jolly-Seber open population model to estimate survival of several feeding groups in Alaska and reports rates ranging from 0.85 to 1.02 for different feeding groups. Model assumptions were violated, however, so this range of survival rates is likely biased and includes values that are not plausible (i.e., survival rate >1).

Humpback Whale Recovery Planning

The humpback whale, which was listed as endangered throughout its range in 1970, is one of three large whale species for which a recovery plan exists. The Humpback Whale Recovery Plan, finalized in 1991, aims to increase humpback whale populations to at least 60% of either the number existing before commercial exploitation began (i.e., historical carrying capacity), or the current carrying capacity of the environment. Because an accurate estimate of carrying capacity is not available, an interim numerical goal in the recovery plan was to double existing population sizes within the subsequent 20 years, which admittedly is rather arbitrary. Despite the ESA requirement to include "objective, measurable criteria which, when met, would result in a determination. . .that the species be removed from the List" (Endangered Species Act of 1988), the recovery plan states that "This plan cannot now identify specific target population sizes at which downlisting might be considered" (NMFS 1991: 33). Although the recovery plan does not include explicit or quantitative classification criteria, it does recommend the timely development of and agreement on criteria for making classification decisions.

The classification criteria recently proposed by the World Conservation Union (World Conservation Union [IUCN] 1994) provide quantitative criteria for classification of species on the Red List of Threatened and Endangered Wildlife. Although these criteria also include an emphasis on using quantitative criteria, they are primarily oriented toward terrestrial species and are difficult to apply to marine species. In particular, the IUCN criteria are generally not appropriate because parameters such as "extent of occurrence" or "degree of fragmentation" are quantifiable only with great difficulty in the marine realm, particularly for highly migratory species such as humpback whales. Further, the IUCN criteria do not explicitly incorporate uncertainty in available data. Currently, the entire worldwide species of humpback whales is classified as vulnerable by IUCN, which one might equate to threatened under the ESA.

Our proposed classification criteria are meant to encompass the factors specified by the ESA as components of a species' status (habitat loss, overutilization, disease or predation, regulatory mechanisms, and "other influences"). Although the precise influence of each of these

factors on the continued persistence of humpback whales is unknown, the combination of these factors is ultimately reflected in the population growth rate and the population size. Our classification therefore encompasses these factors by incorporating uncertainty associated with population size and trend (for review of humpback whale endangerment in the context of the five ESA factors, see Gerber 1998*b*).

Methods

General Approach to Classification of Large Whales

Four basic types of data should be used in developing classification criteria for North Pacific humpback whales: abundance, trends in abundance, changes in distribution, and regulatory status. To put these principles into practice, a workshop was convened in January 1997 at which a consensus was sought regarding classification criteria (Gerber & DeMaster 1997). Participants in this workshop represented expertise in large whale biology, population ecology, population modeling, and population viability theory. There was agreement among participants that uncertainty in data should be incorporated into any management decisions such that classification criteria would be more conservative where data are limited or unavailable. It was also agreed that an appropriate classification framework would avoid arbitrary guesses and instead rely on existing data or at least data that could be collected in the near future. It was suggested that criteria should be developed independently of assumptions about population structure and that levels of risk associated with different assumptions about population structure should be made explicit.

The classification criteria developed for humpback whales include downlisting criteria for endangered to threatened and from threatened to delisted. For either decision, the criteria require that an international regime be in place and be effective in regulating human-related disturbance and mortality. Conditions for downlisting from endangered to threatened are that all designated wintering and feeding areas will maintain a population size such that over the next 10 years there is a high probability that abundance will remain above a specified critical level (N_q) and a high probability that abundance will remain below the threshold for threatened status (N_{th}). Conditions for delisting are that all designated wintering and feeding areas will maintain a population size such that over the next 25 years there is a high probability that abundance will remain above the threshold level for endangered (N_{end}) and a high probability that abundance will remain above N_{th}.

The term *designated* for wintering and feeding areas is intended to imply that multiple population-structure hypotheses may be considered. The critical level (N_q) is defined as the population size for which it is too late for management to prevent extinction (i.e., the quasiextinction level). The risk of extinction of any population is a quantitative assessment of how likely a population is to fall below N_q during some specified time period. Clearly, larger populations will be less likely to decline to N_q during any time interval than will smaller populations, all other trend-determining factors being equal. We defined two thresholds relating to the likelihood of falling to N_q. First, we defined N_{end}, the threshold level for endangered status, as the population level necessary to maintain a high probability of remaining above N_q for 10 years. Similarly, we defined N_{th}, the threshold level for threatened status, as the population level necessary to maintain a high probability of remaining above N_{end} for 25 years. Specifically, threshold levels for endangered and threatened can be written as

$$N_{end} = N_t \text{ such that probability } (N_0...N_{10} > N_q) = 0.95$$
$$\text{and}$$
$$N_{th} = N_t \text{ such that probability } (N_0...N_{35} > N_{end}) = 0.95,$$

where N_q is the critical level (e.g., 500 individuals), N_0 is the initial population size, and N_t is the population size at time t.

The threshold for endangered status is equivalent to a 0.05 probability of a population at N_{end} being at or below N_q after 10 years, and the threshold for threatened status is equivalent to a 0.05 probability of a population being at N_{th} or below N_{end} in 25 years. The 0.05 probability specified in the criteria may be changed depending on what is considered an acceptable level of risk. Further, the selection of appropriate time periods should be approved by the policymakers responsible for management.

The criteria are intended to be applicable to a variety of types and levels of data quality and to incorporate a precautionary approach. According to this classification framework, N_{end} and N_{th} are case-specific and dependent upon available abundance, population structure, and trend data. To apply these ideas to the question of how to classify North Pacific humpback whales, we assumed that whale population trends can be approximated by the equation $N_t = N_0\lambda^t$ where λ is the discrete annual rate of population change. Recognizing that λ is not a known constant but rather a random variable with a probability distribution (due to uncertainty in its estimation or to temporal variability in the environment), our criteria can be expressed as follows (equations 1 and 2):

if $\lambda_{(0.05)} < 1$ then $N_{end} = N_q \times (\lambda_{(0.05)})^{-10}$, and
$$N_{th} = N_{end} \times (\lambda_{(0.05)})^{-25} = N_q \times (\lambda_{(0.05)})^{-35}, \quad (1)$$

where N_q is 500 for humpback whales and $\lambda_{(0.05)}$ is the fifth-percentile λ from our distribution of possible λs, and

if $\lambda_{(0.05)} \geq 1$ then $N_{end} = N_q$ and $N_{th} = N_{end}$. \quad (2)

Thus, to incorporate the specific effect of uncertainty in our estimate of N_{end} and N_{th}, we used the lower fifth percentile of a distribution of λ values, corresponding to our stated goal of maintaining at least a 0.95 probability of remaining above N_q over the next 10 and 35 years for N_{end} and N_{th}, respectively. If $\lambda_{(0.05)} > 1$, it is unlikely that the population will decline in the specified timeframe. Therefore, the condition that $N_{th} = N_{end}$ when $\lambda_{(0.05)} > 1$ is reasonable.

The distribution of lambda values may be calculated using trend data or demographic data. Given the lack of time series of abundance estimates for humpback whales, we based the solution for N_{end} and N_{th} on a population growth model that incorporates uncertainty in demographic data from two sources: sampling error and temporal variability in the environment. Solving equation 1 for several different $\lambda_{(0.05)}$ values reveals the precautionary nature of the approach: as uncertainty regarding λ increases, the distribution around mean λ values widens (meaning that $\lambda_{(0.05)}$ becomes smaller) and threshold levels for classification as endangered and threatened increase.

An estimate of N_q for humpback whales should represent the lower limit for a population, below which management could not prevent extinction. This is a difficult parameter to estimate when empirical data are limited and theoretical approaches are in dispute. Because there is a great deal of uncertainty concerning the ability of large vertebrates to recover from very low population densities, our choice of N_q was based on ancillary data from the conservation biology literature and on the con-

sensus of a panel of whale experts (Best 1993; Gerber & DeMaster 1997). As an initial approach, we assumed an N_q value of 500 animals. This was based on the observation that hunting reduced two stocks of northern right whales to <500 animals each; although anthropogenic mortality from ship strikes and entanglement persists today, these populations have shown little sign of recovery over the past several decades, whereas other larger populations of whales have increased in number. Given the uncertainty regarding the relative effect of anthropogenic and small population effects that limit the recovery of large whales, we also tested the sensitivity of threshold values to assumed N_q values of 650 and 1000 (Fig. 1). The value of 650 is based on a minimum viable population size estimated by the approach of Ralls et al. (1983), which incorporates variance in sex ratio and percent immature but does not incorporate the effect of fluctuation in population size.

Modeling Approach for Humpback Whales

According to our proposed classification framework, uncertainty associated with available scientific information can be incorporated into delisting criteria through the use of probability statements, such that it is left to the manager to decide the appropriate level of risk for each level of threat (endangered or threatened). Therefore, the absence of data does not preclude the establishment of classification criteria. This approach implies a built-in precautionary mechanism that places the burden of proof on the agency to gain necessary population data
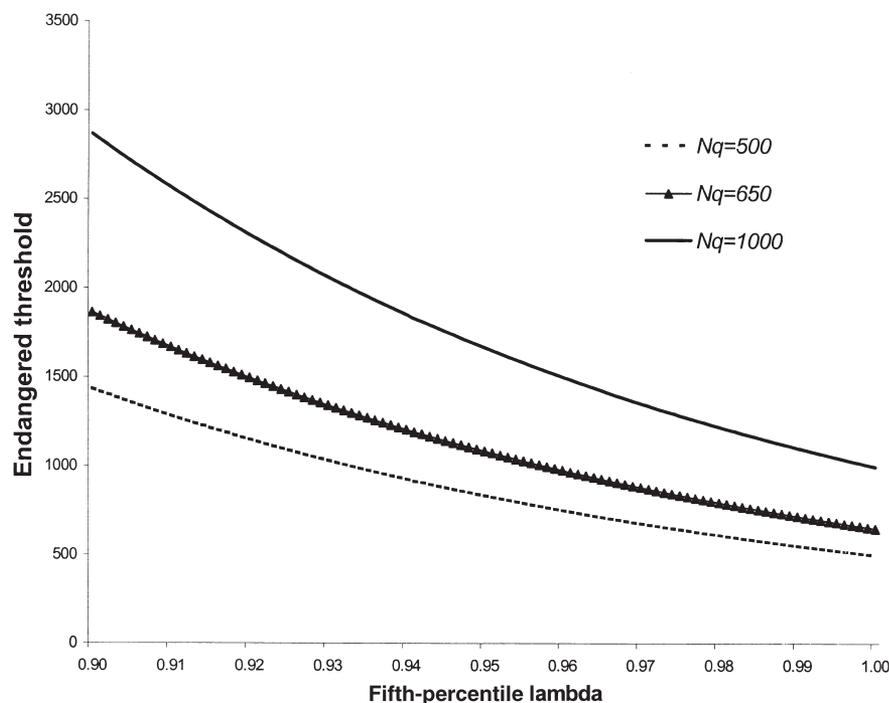

Figure 1. Relationship between estimates of N_{end} and assumed N_q values of 500, 650, and 1000 for any species considered under the Endangered Species Act classification scheme.

before a population can be considered for delisting. The importance of such an approach is that classification criteria may guide managers in focusing research and monitoring efforts to gather data necessary for more refined classification decisions.

We now consider explicitly the data available for humpback whales in order to demonstrate how different types of data could be analyzed given our proposed classification scheme (Fig. 2). First, no reliable data exist for population size over time, so standard extinction risk models cannot be applied (Dennis et al. 1991; Lande 1993). Considering the data available for humpback whales in the North Pacific, our approach should rely on what little demographic data we do have for humpback whales. Specifically, we used a stochastic, age-structured projection model, with estimation error and environmental stochasticity contributing to our uncertainty in survival and fecundity rates. This model produced a frequency distribution of λ values (after 1000 independent simulations) which then could be used to identify the $\lambda_{(0.05)}$ values central to our approach. Uncertainty was incorporated into the procedure in two ways: sampling error that
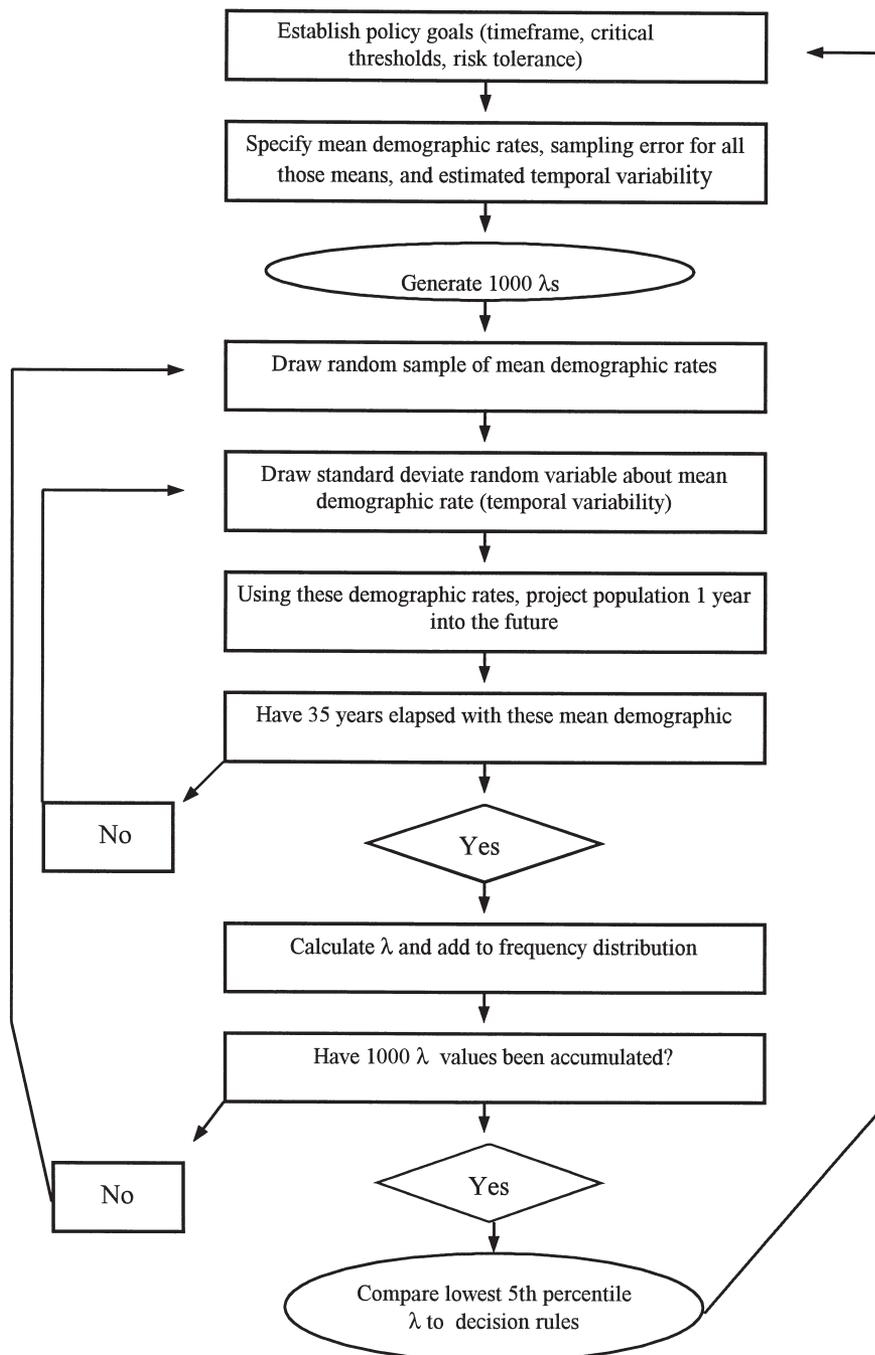

Figure 2. Schematic diagram of algorithm for simulation model used for Endangered Species Act classification of humpback whales.

yields uncertain estimates of mean fecundity and survival rates and environmental variability that reflects year-to-year variation about mean demographic rates due to the vicissitudes of the environment. Before describing how we estimated the magnitude of these uncertain parameters, we describe the general modeling approach.

We used an age-structured model to attain a realized stochastic annual rate of change (denoted by the Kth root of N_{t+k}/N_t, as realized by each stochastic trajectory; Caswell 1989) by drawing for each year a different suite of demographic parameters and simulating population growth 35 years into the future. To obtain the initial age-structured population common to all simulations, we used the Lotka equation to calculate the right eigenvector corresponding to the average deterministic λ value (1.058). Each trajectory was then started at the stable age distribution for a population of 6000 associated with that deterministic λ. To obtain probability distributions for the stochastic λ, we repeated the simulations 1000 times. By making 1000 such draws, we used a Monte Carlo approach to generate a probability distribution for realized rates of population change. Monte Carlo simulations were conducted where rates were drawn randomly within a prespecified distribution. We assumed that environmental fluctuations in survival were correlated over all age classes, as were fluctuations in fecundity. Thus if the survival of 4-year-old whales were 0.05 SD better than average in a given year, so too was the survival of other age classes. In other words, the environmental fluctuations were assumed to act identically on all age classes.

Estimating Mean Demographic Rates and Sources of Variation

We used Straley's (1994) data on birth interval to estimate fecundity rates of humpbacks. To eliminate the bias toward observing only short birth intervals, we used data only from whales that were seen for at least 10 consecutive years. With this censored data we obtained a mean birth interval of 2.31 (SE = 0.26) and a corresponding annual birth rate of 0.43 (SE = 0.075) (Gerber 1998*a*). Because we have no information on age-specific variation in fecundity, we assigned this rate identically to ages 8–34.

Survivorship data were available from a mark-recapture study conducted by Straley (1994). Straley (1994) used a Jolly-Seber open-population model to estimate survival of several feeding groups in Alaska and reported rates ranging from 0.85 to 1.02 for different feeding groups. The apparent biases in these estimates may result from temporary or permanent emigration mimicking mortality, thus lowering survival estimates, and re-immigration mimicking survival or from heterogeneous capture probabilities increasing survival estimates. Using Straley's data, we assumed that survival was independent of age and was adequately described by a uniform distribution with bounds of 0.85 and 0.99, although this distribution should be revised as more precise demographic data become available (e.g., a normal distribution centered on a maximum likelihood estimate for survival). Given that survival rates of adult whales generally range from 0.90 to 0.98 (de la Mare 1985; Buckland 1990; Givens et al. 1995), Straley's estimates, although imprecise, provide a conservative range of possible survival rates for North Pacific humpback whales.

Uncertainty in the Projection Model

Estimating uncertainty due to sampling error is straightforward. For birth interval we took advantage of the fact that this interval is a geometric random variable with p_t equal to the inverse of the birth interval. We used Monte Carlo simulations to sample random draws and evaluated how many draws had to be made before p_t was exceeded. Thus the number of draws is a geometric random variable and corresponds to a sampled birth interval, which in turn can be directly converted into a fecundity value. This approach allowed us to evaluate the range of fecundity values that are likely given a geometric sampling process. To obtain distributions for survival rate uncertainty, we conducted Monte Carlo simulations with random draws from a uniform distribution between 0.85 and 0.99.

A second source of uncertainty is that the environment may vary from year to year, and in doing so alter demographic rates. Although we had enough information to estimate sampling errors for demographic rates, there are no data to estimate the effect of environmental variability on humpback whales. In general, large whales are thought to be relatively resilient to year-to-year fluctuations in the environment (Katona & Whitehead 1988; Clapham et al. 1999). Thus, we assumed that coefficients of variation for changes in annual demographic rates were likely to be <20%, with 5% being a low level, 10% being a moderate level, and 20% representing a scenario of unusually high environmental variability. The environmental variability was incorporated by random draws from Gaussian random variables with coefficients of variation of 0.05, 0.10, and 0.20 added to the mean demographic rates that were generated by the sampling error process (Fig. 2).

Results and Discussion

Given our proposed criteria, a population can be considered for downlisting when an international regime is in place and is effective in regulating human-related disturbance and mortality. Since 1966, humpback whales have been protected from commercial whaling based on a moratorium mandated by the IWC. Populations of humpback whales in U.S. waters are also protected un-

der the auspices of the Marine Mammal Protection Act. The current regime is therefore considered effective in regulating the disturbance and mortality of humpback whales, and a mechanism is in place that ensures continued monitoring. Because current regulations appear to adequately regulate human-related mortality of humpbacks and because good monitoring programs are in place, it makes sense to turn to quantitative population data and ask whether there is evidence to support downlisting. The key to this data-oriented downlisting analysis is handling the enormous uncertainty in available data for humpback whales.

Our three scenarios produced relatively high mean values for the stochastic asymptotic rate of population growth: 1.07, 1.065, and 1.045 for low, medium, and high environmental variability, respectively. The addition of variability led to moderate reductions in mean stochastic λ, as expected by theory (Caswell 1989). But the mean values were not the focus of our analysis. Rather, we were concerned with the distribution of λ values about these means (Fig. 3), in particular the lowest 5% of the λ values. For the different variability scenarios, the $\lambda_{(0.05)}$ values are 0.980, 0.948, and 0.898 for low, medium, and high variability, respectively (Table 1). Thus, although we expect that humpback whales in the North Pacific will continue to increase in abundance, there is still a 5% chance that they could decrease by as much as 10% annually (for the high-variability scenario). Finally, we can use these $\lambda_{(0.05)}$ values to calculate threshold values for downlisting or delisting (Table 1). The threshold levels for the low-, medium-, and high-variability scenarios were 610, 850, and 1470 for N_{end} and 1010, 3240, and 21,590 for N_{th}. Obviously, if we could reduce uncertainty and thus the scatter of λ values about the mean, these downlisting and delisting thresholds could be reduced.

To determine what the results of our modeling effort mean for today's humpback whale population, we can use the recent abundance estimates reported by Calambokidis et al. (1997) in the context of our analytic solution for N_{end} (equations 1–2). To incorporate uncertainty in abundance, we considered the lower bound of the estimated 95% confidence interval for the best estimate in our classification scheme (N_{min}). If we assumed one population unit for North Pacific humpbacks, the probability that the lower bound of the estimated population size (5081) would decline below the critical threshold in 10 years is >0.05 if $\lambda_{(0.05)} \leq 0.79$. Thus, because the estimated lower bound of the population growth rate ($\lambda_{(0.05)}$) from all three scenarios was >0.79, our analysis is consistent with a recommendation to downlist from endangered to threatened. Following the same procedure, however, the probability that the estimated population size of 5081 would decline below the threshold for threatened in 25 years is >0.05 for the high environmental variability scenario and <0.05 for the low and
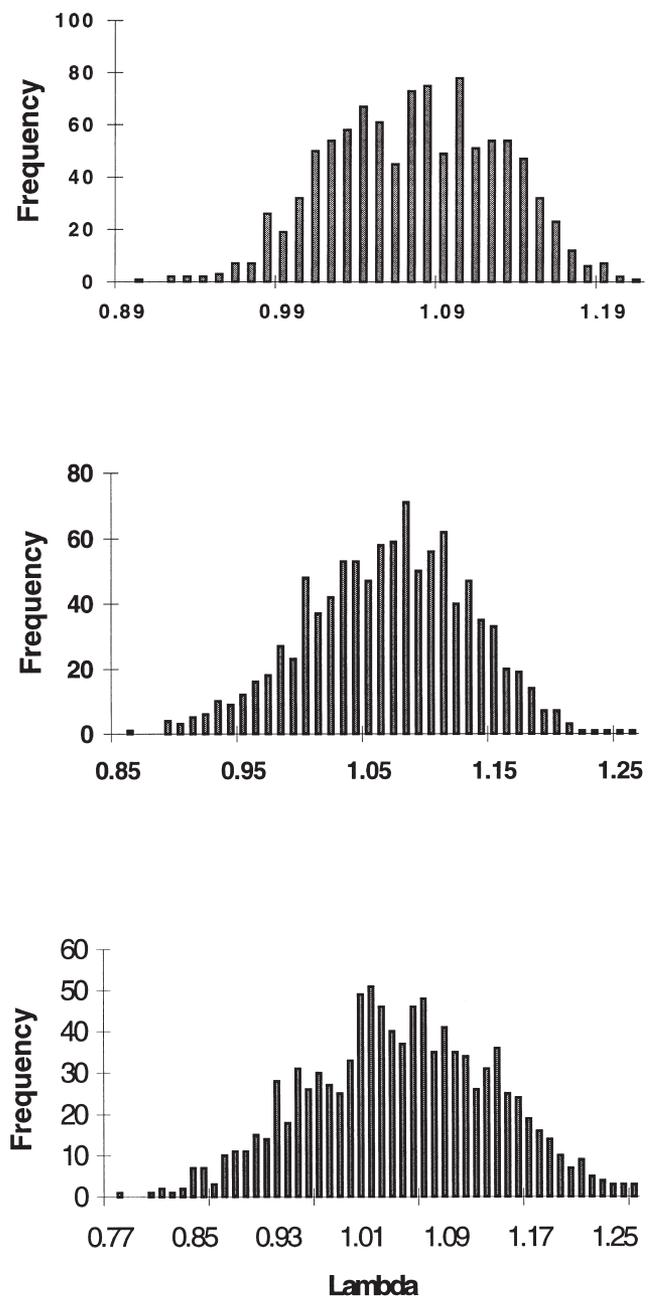

Figure 3. Frequency distributions for lambda resulting from stochastic population trajectories that incorporate measurement error and environmental variability in demographic parameters for humpback whales. Distributions include (from top to bottom) a low environmental variability scenario (CV [coefficient of variation] = 0.05, SE fecundity = 0.046, SE survival = 0.022), a moderate environmental variability scenario (CV = 0.10, SE fecundity = 0.093, SE survival = 0.043), and a high environmental variability scenario (CV = 0.20, SE fecundity = 0.185, SE survival = 0.087).

Table 1. Statistics and $\lambda_{(0.05)}$ from distribution of λ values estimated with Monte Carlo simulations of the effects of high, moderate, and low levels of environmental variability on demographic parameters of humpback whales.

	Environmental variability		
	low[a]	*moderate[b]*	*high[c]*
$\lambda_{(0.05)}$	0.980	0.948	0.898
Median	1.070	1.065	1.047
Mean	1.067	1.060	1.047
Variance	0.002	0.004	0.008
Kurtosis	−0.481	−0.186	−0.353
N_{end}	610	850	1470
N_{th}	1010	3240	21590

[a]*CV (coefficients of variation) = 0.05, SE fecundity = 0.046, SE survival = 0.002.*
[b]*CV = 0.10, SE fecundity = 0.093, SE survival = 0.043.*
[c]*CV = 0.20, SE fecundity = 0.185, SE survival = 0.087.*

medium environmental variability scenarios. Until empirical data become available (which will allow us to quantify true environmental variability), we recommend that, because the most conservative $\lambda_{(0.05)}$ value resulting from our three scenarios was less than the threshold $\lambda_{(0.05)}$ (i.e., 0.94, Table 2), delisting of North Pacific humpback whales under the single-stock scenario should not be considered at this time.

Alternatively, we can consider additional hypotheses about population structure in the context of our classification scheme. For example, if we assume that the North Pacific population of humpback whales includes three management units based on breeding areas, $\lambda_{(0.05)}$ for the eastern, central, and western populations must be ≥0.93, 0.83, and 1.00, respectively, for downlisting from endangered to threatened for the three populations (Table 2). For delisting, $\lambda_{(0.05)}$ must be ≥0.98, 0.95, and 1.00, respectively, for the three populations (Table 2). In this case, the data are consistent with a recommendation to downlist the central population to threatened but to maintain an endangered classification for the western and eastern populations. The effect of alternative population-structure scenarios on the ESA status of North Pacific humpbacks includes a more conservative classification for smaller population units (Table 3).

The results of our simulation scenarios may be used to evaluate the $\lambda_{(0.05)}$ resulting from consideration of different distributions for fecundity and survival rates. We considered the lower bound of this range of values and that an international regime is in place and is effective in regulating human-related disturbance and mortality. Thus, our results are consistent with a recommendation that the North Pacific humpback whale should be downlisted from endangered to threatened, but not delisted, if we assume that the North Pacific population is one management unit. If we assume three management units and apply the estimate of $\lambda_{(0.05)}$ for the central population to the other two populations, the eastern and western stocks should remain listed as endangered and the central stocks should be downlisted from endangered to threatened.

Where the N_q value is increased to either 650 or to 1000, our recommendations regarding downlisting do not change under any of the population-structure scenarios (Fig. 1). If we considered alternate time frames, such as 25 and 50 years instead of 10 and 35 years, all population units would remain listed as endangered for the high environmental variability scenario. This is because the lower bound of the population growth rate necessary for reclassification from endangered to threatened (Table 2) increases for longer time periods. If, however, we had not incorporated uncertainty in abundance (i.e., by considering the "best" abundance estimate, N_{best}, rather than N_{min}), our recommendations would hold in all scenarios with the exception of the eastern population, which would be downlisted to threatened because N_{best} (1611) > N_{end} (Tables 1 & 2). Thus, with precise abundance estimates, downlisting this population to threatened could be considered, even under a wide range of possible time frames.

Once an explicit protocol is in place, such as that represented by equations 1 and 2, it is straightforward to ask how robust are ESA classification decisions. For example, consider our recommendation to downlist the whole North Pacific population because it is unlikely to decline below N_q under our three assumed levels of environmental variability. Because we do not know what the true environmental variability is for North Pacific humpbacks, we can ask what coefficients of variation

Table 2. Lower bound of population growth rate ($\lambda_{(0.05)}$) necessary for reclassification from endangered to threatened and threatened to delisted for a range of abundance estimates assuming one and three stocks of North Pacific humpback whales.*

	Current population size					
					3 population units	
		1 population unit		eastern stock	central stock	western stock
Threshold $\lambda_{(0.05)}$	$N_{min} = 5081$	$N_{min} = 7000$	$N_{min} = 8000$	$N_{min} = 1017$	$N_{min} = 3243$	$N_{min} = 328$
Endangered	0.79	0.77	0.76	0.93	0.83	>1.00
Threatened	0.94	0.93	0.92	0.98	0.95	>1.00

Given equations 1 and 2 (in text), if $\lambda_{(0.05)} \geq 1$, $N_{end} = N_q = N_{th}$ where $N_q = 500$ for humpback whales. Thus, because N_{min} for the western stock ≤500, $\lambda_{(0.05)} > 1.00$.

Table 3. Endangered Species Act classification of North Pacific humpback whales for different scenarios of population structure.

Population structure assumption	Abundance (N_{min})	Reference	Resulting status recommendation
Entire North Pacific Ocean basin	5081	Calambokidis et al. 1997	threatened
Breeding unit as population		Calambokidis et al. 1997	
western	328		endangered
central	3243		threatened
eastern	1017		endangered
Breeding unit as population		Calambokidis et al. 1997; Barlow 1994	
western	328		endangered
central	3243		threatened
eastern-mainland	808		endangered
eastern-offshore	unknown		endangered
Feeding unit as population		Barlow 1994; Straley 1994; Waite et al. 1999	
California–British Columbia	808		threatened
southeast Alaska	350		endangered
Prince William Sound	unknown		endangered
Kodiak	406		endangered
Aleutian Islands–Kamchatka	unknown		endangered

(CV) in survival and fecundity would be large enough that the $\lambda_{(0.05)}$ does not exceed 0.79. We ran a series of simulations and found that this CV would have to be 0.40 before the lowest $\lambda_{(0.05)}$ was so low that downlisting would not be recommended. The major "guess" in our analysis is the plausible range of temporal variability in λ for humpback whales (represented here as the CV). By being explicit about how we make our decisions, biologists and managers can ask themselves how likely it is that the CV for humpback whale demographic rates exceeds 40%. Values this large or larger are unlikely for most long-lived vertebrates, including the humpback whale.

Contentious Points Regarding Reclassification Decisions

Any decision to downlist or delist a species is likely to be fraught with controversy. For example, we have assumed arbitrarily that using the $\lambda_{(0.05)}$ from the distributions is adequate in evaluating whether the current population can reasonably be considered to remain above N_{end} or N_{th} over the next 10–35 years. There is nothing magical about this value, and policymakers should be encouraged to comment on whether this value is overly restrictive, too aggressive, or appropriate.

One virtue of an explicit approach, such as that we propose, is that it focuses the debate on critical scientific points as opposed to ideology. For humpback whales, it is valuable to ask about the major gaps in knowledge that leave the door open to fractious debate. First, it will be necessary to determine the appropriate management unit for North Pacific humpback whales before reclassification is initiated. Genetic samples and photo-identification studies should continue for all feeding and breeding units. Also, further thought should be given to the sample size necessary to detect population subdivisions based on expected genetic diversity.

Second, a significant uncertainty in our proposed classification criteria is in the assumption of 500 as the population's quasi-extinction level. To use the MVP approach described by Ralls et al. (1996), detailed data on the age structure and sex ratio of North Pacific humpback whales are needed. Such an estimate is highly sensitive to the operational sex ratio of breeding animals, a parameter not well understood for North Pacific humpbacks. Even with perfect information, it may not be possible to estimate such a number with any confidence. For example, Lande (1994) suggested that a minimum viable effective population of 5000, rather than 500 (Franklin 1980), is necessary to maintain normal levels of genetic variance under a balance between mutation and random genetic drift. The minimum viable effective population may also vary with the number and size of designated populations (which is dependent upon the tendency of whales to aggregate in feeding and wintering grounds), reflecting differences in genetic diversity. Although it may be possible to develop a multiplier for converting the effective population size to the actual population size, in light of the controversy over a suitable value for effective population size and the lack of adequate data on, for example, sex ratio, age structure, and fluctuation in population size, we arbitrarily used 500 as an initial value for N_q. Given the current state of knowledge of dynamics of populations at low densities among large whales, assuming 500 as N_q is a reasonable starting point. Nonetheless, we recommend that this parameter estimate be reexamined as more detailed data become available.

Third, a key component of our proposed classification criteria is the gathering of data that could better substantiate that populations have recovered and are unlikely to become extinct within the foreseeable future. In particular, systematic surveys should be conducted to estimate abundance and demographic information for stocks of North Pacific humpback whales. An alternate and perhaps more direct approach would be to obtain a second abundance estimate, which would allow λ to be calculated based on the change in abundance over the appropriate time period.

Although no method can compensate for information gaps, an explicit classification scheme can illuminate what information is most needed for effective conservation. In addition, a quantitative classification scheme permits identification of the precise injections of uncertainty that have produced the spread in a given distribution of population growth rates that prevents delisting (because the scatter around the mean is wide) or identification of which reductions in uncertainty have led to a decision to downlist. Finally, our approach makes clear the value of better information: delisting could occur only if data are adequately precise to indicate a <5% chance of a population decline sufficient to drive a population to N_q in 10–35 years. We cannot say whether the proposed classification criteria are the "right answer," but at least by being explicit in our reasoning such quantitative approaches are subject to scientific scrutiny and rejection. The development of this type of explicit and quantitative approach from which mistakes can be identified and learned from is critical to effective conservation of threatened and endangered species. Analyses similar to those we conducted should be initiated for other taxonomic groups for which ESA listing and recovery decisions are relevant.

Acknowledgments

Literature Cited

Baker, C. S., A. Perry, and L. M. Herman. 1987. Reproductive histories of female humpback whales, *Megaptera novaeangliae*, in the North Pacific. Marine Ecology Progress Series **41:**103–114.

Barlow, J. 1994. Recent information on the status of large whales in California waters. Technical memorandum NMFS-SWFSC-203. National Ocean and Atmospheric Administration, Seattle.

Barlow, J., and P. J. Clapham. 1997. A new birth-interval approach to estimating demographic parameters of humpback whales. Ecology **78:**535–546.

Best, P. B. 1993. Increase rates in severely depleted stocks of baleen whales. ICES Journal of Marine Science **50:**169–186.

Brownell, R. L., Jr., K. Ralls, and W. F. Perrin. 1989. The plight of the "forgotten" whales. Oceanus **32(1):**5–11.

Buckland, S. T. 1990. Estimation of survival rates from sightings of individually identifiable whales. Reports of the International Whaling Commission **12:**149–153.

Calambokidis, J., et al. 1996. Interchange and isolation of Humpback whales off California and other North Pacific feeding grounds. Marine Mammal Science **12(2):**215–226.

Calambokidis, J., et al. 1997. Abundance and population structure of humpback whales in the North Pacific basin. Final contract report 50ABNF100113. Southwest Fisheries Science Center, La Jolla, California.

Caswell, H. 1989. Matrix population models: construction, analysis and interpretation. Sinauer Associates, Sunderland, Massachusetts.

Clapham, P. J. 1992. The age at attainment of sexual maturity in humpback whales, *Megaptera novaeangliae*. Canadian Journal of Zoology **70:**1470–1472.

Clapham, P. J., and C. A. Mayo. 1987. The attainment of sexual maturity in two female humpback whales. Marine Mammal Science **3(3):**279–283.

Clapham, P. J., S. B. Young, and R. L. Brownell. 1999. Baleen whales: conservation issues and the status of the most endangered populations. Mammal Review **29(1):**35–60.

de la Mare, W.K. 1985. On the estimation of mortality rates from whale age data, with particular reference to minke whales (*Balaenoptera acutostrata*) in the Southern Hemisphere. Reports of the International Whaling Commission **35:**239–250.

Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs **61(2):**115–143.

Endangered Species Act of 1973 (Pub. L. 93-205, 81 Stat. 884, Dec. 28, 1973).

Endangered Species Act of 1988 (Pub. L. 100-478, Oct. 7, 1988).

Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135–149 in M. A. Soulé and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachusetts.

Gerber, L. R. 1998*a*. Risk analysis and use of stochastic population models for determining the Endangered Species Act status of North Pacific marine mammals. Ph.D. dissertation. University of Washington, Seattle.

Gerber, L. R. 1998*b*. Seeking a rational approach to setting conservation priorities for marine mammals. Integrative Biology **1:**212–221.

Gerber, L. R., and D. P. DeMaster. 1997. Endangered Species Act classification criteria for North Pacific humpback whales. Pages 203–211 in P. S. Hill and D. P. DeMaster, editors. Marine Mammal Protection Act and Endangered Species Act implementation program 1996. Processed report 97-10. Alaska Fisheries Science Center, Seattle.

Givens, G. H., J. E. Zeh, and A. E. Raftery. 1995. Assessment of the Bering-Chukchi-Beaufort Seas stock of Bowhead whales using the BALEEN II model in a Bayesian synthesis framework. Reports of the International Whaling Commission **45:**345–364.

Hill, P. S., D. P. DeMaster, and R. J. Small. 1997. Humpback whale (*Megaptera novaeangliae*). Pages 135–149 in Alaska marine mammal stock assessments 1996. National Oceanic and Atmospheric Association technical memorandum. National Marine Fisheries Service, Seattle.

Katona, S. K., and J. H. Beard. 1990. Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. Reports of the International Whaling Commission Special Issue **12:**295–305.

Katona, S., and H. Whitehead. 1988. Are cetacea ecologically important? Oceanography and Marine Biology Annual Review **26:**553–568.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist **142:**911–927.

Lande, R. 1994. Mutation and conservation. Conservation Biology **9:** 782–791.

Larsen, A. H., J. Sigurjónsson, N. Óien, G. Vikingsson, and P. J. Palsbøll. 1996. Population genetic analysis of mitochondrial and nuclear genetic loci in skin biopsies collected from central and northeastern North Atlantic humpback whales (*Megaptera novaeangliae*): population identity and migratory destinations. Proceedings of the Royal Society of London **263:**1611–1618.

National Marine Fisheries Service. 1991. Final national recovery plan for the humpback whale (*Megaptera novaeangliae*) in waters of the United States of America. Silver Spring, Maryland.

Palsbøll, P. J., et al. 1997. Genetic tagging of humpback whales. Nature **388:**767–769.

Palsbøll, P. J., P. J. Clapham, D. K. Mattila, F. Larsen, R. Sears, H. R. Siegismund, J. Sigurjónsson, O. Vásquez, and P. Arctander. 1995. Distribution of mtDNA haplotypes in North Atlantic humpback whales: the influence of behavior on population structure. Marine Ecology Progress Series **116:**1–10.

Ralls, K., D. P. DeMaster, and J. A. Estes. 1996. Developing a criterion for delisting the southern sea otter under the U.S. Endangered Species Act. Conservation Biology **10:**1528–1537.

Ralls, K., J. Ballou, and R. L. Brownell. 1983. Genetic diversity in California sea otters—theoretical considerations and management implications. Biological Conservation **25(3):**209–232.

Straley, J. M. 1994. Seasonal characteristics of humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. M.S. thesis. University of Alaska, Fairbanks.

Straley, J. M., C. M. Gabriele, and C. S. Baker. 1994. Annual reproduction by individually identified humpback whales (*Megaptera novaeangliae*) in Alaska waters. Marine Mammal Science **10:**87–92.

U.S. Fish and Wildlife Service. 1996. Policy regarding the recognition of distinct vertebrate population segments under the Endangered Species Act. U.S. Fish and Wildlife Service, Washington, D.C.

Waite, J. M., M. E. Dahlheim, R. C. Hobbs, S. A. Mizroch, O. V. Ziegesar-Matkin, J. M. Straley, L. M. Herman, and J. Jacobson. 1999. Evidence of a feeding aggregation of humpback whales (*Megaptera novaeangliae*) around Kodiak Island, Alaska. Marine Mammal Science **15(1):**210–219.

World Conservation Union. 1994. IUCN red list categories. World Conservation Union, Gland, Switzerland.