Rethinking the Stock Concept: A Phylogeographic Approach

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Abstract: *The "stock" is the fundamental population unit of legally mandated conservation efforts, yet its formal definition in the scientific literature and in two U.S. conservation acts is varied and so general that attempts to apply it in practice are arbitrary. Because choice of stocks deserving management protection is sometimes politically contentious, improvement of the working definition is important.*

A key element should be the degree to which a population can be considered an evolutionarily significant unit. We propose that a hierarchial classification scheme be applied to stock designations. Category I populations, having the highest probability of being evolutionarily significant units, are characterized by a discontinuous genetic divergence pattern where locally adapted and closely related genome assemblages are separated from others geographically and by significant genetic distances. Category II populations are similarly characterized by significant genetic diversity, but with weak geographic partitioning. Category III populations are the converse of II, having little genetic differentiation between assemblages that are clearly separate and likely to be reproductively isolated. Category IV assemblages have the lowest probability of being evolutionarily significant units and are characterized by extensive gene flow and no subdivision by extrinsic barriers. In addition to phylogeographic designation, the following information is used in the classification, as indicated by single-letter abbreviations: distribution (a), population response (b), phenotypic (c), and

Resumen: *El stock es la unidad poblacional fundamental para los esfuerzos de conservación requeridos por ley, sin embargo, su definición formal en la literatura científica y en dos actas de conservación de los Estados Unidos es diversa y tan general que cualquier intento para usarlo en la práctica es arbitrario. Dado que la elección de los stocks merecedores de protección en su manejo es a veces un hecho políticamente contencioso, es muy importante mejorar la definición en uso.*

Un elemento clave debería ser el grado en que una población puede ser considerada como una unidad evolutivamente significativa. Proponemos que se aplique un esquema jerárquico de clasificación a la desiganción de stocks. La Categoria I, poblaciones con la mayor probabilidad de ser unidades evolutivamente significativas, son caracterizadas por un patrón discontinuo de divergencia genética donde agrupaciones de genomas localmente adaptados e íntimamente relacionados están geográficamente aislados y separados de otros por distancias genéticas significativas. La Categoria II está también caracterizada por una significativa diversidad genética pero con una débil subdivisión geográfica. La Categoria III es la inversa de II, poseyendo una pequeña diferenciación genética entre agrupaciones que están claramente separadas y probablemente están aisladas reproductivamente. Las agrupaciones dentro de la Categoria IV, que tienen la menor probabilidad de ser unidades evolutivamente significativas, están caracterizados por un flujo génico extensivo y por una ausencia de subdivisión a través de barreras extrínsecas. Además de desiganciones filogeográficas, la información usada para clasificar también

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genotypic *(d) information. Included are evidence both for and against designating population as a separate stock. In the designation "Type II a/bc," for example, information to the right of the solidus would be evidence for "lumping," to the left would be for "splitting." Missing letter abbreviations would signify lack of reliable data. Note that phylogeographic designation depends on the results of selection operating to produce a locally adapted genome (indicated by differences in demographic, phenotypic, and genotypic measures) and on gene flow (indicated by differences in distribution or by movement data).*

Hierarchial stock categorization allows resource managers to direct limited resources to the populations most deserving of protection, that is, the populations that are most likely to be evolutionarily significant units. Using this comprehensive classification of stock allows preliminary, conservative splitting of assemblages where data are lacking without the danger that these divisions will become entrenched as biological dogma.

debería ser incluída usando abreviaciones con letras: distribución (a), respuesta poblacional (b), información fenotípica (c), e información genotípica (d). Se incluiría tanto evidencia a favor como en contra, por ejemplo, "Tipo II a/bc" donde la información a la derecha sería evidencia en favor del "agrupamiento", información a la izquierda sería en favor de la "disociación"; la ausencia de abreviaciones con letras indicaría ausencia de datos confiables. La designación filogenética depende de los resultados de selección natural, que opera para producir un genoma localmente adaptado (indicado por diferencias en mediciones demográficas, fenotípicas, y genotípicas), y del flujo génico (indicado por diferencias en distribución o por datos sobre movimientos).

La categorización jerárquica del sotck permite a los administradores de recursos asignar los limitados recursos a aquellas poblaciones que más necesitan protección, es decir a poblaciones que son, muy probablemente, unidades evolutivamente significativas. El uso de esta clasificación comprensiva de stocks permite una subdivisión preliminar conservadora de las agrupaciones cuando exista falta de datos, sin el peligro de que estas subdivisiones se transformen en dogma biológico.

Introduction

A "population stock," as defined in the Marine Mammal Protection Act of 1972 (MMPA), is a group of animals that share a common space and interbreed; a "vertebrate species," as defined in the Endangered Species Act of 1973 (ESA), is a distinct population segment that interbreeds. The purpose of such definitions in both acts is to direct management efforts to taxon levels below that of the species to ensure that populations that are uniquely adapted to given areas are not irreversibly reduced by harvest or habitat destruction. Although the stock concept is thus codified into law by these environmental acts, no useful working definitions of intraspecific taxa are provided. At the same time, no universally accepted definitions or even pro tem consensus exist among biologists. Thus, much confusion exists among researchers, regulators, users, and conservationists as to what taxon levels conservation efforts are to be directed toward.

The problem with the definitions of stock in the acts is that it is not obvious how to define quantitatively what is meant by either "sharing" or "interbreeding." For example, do we extend protection to the gray squirrels in Central Park in New York? They certainly meet the legislative criteria of sharing a common space and interbreeding. Or if members from two apparently distinct populations of dolphins only interbreed during EL Niño events, should these populations be managed as one management unit? What if their ranges overlap, or they interbreed once every 100 (or 1000) years? Should they then be managed as separate stocks? Of course,

there are no indisputable answers to these questions. It is absurd to apply a rigid, typological definition of stock in such situations, because at present there is no way to determine how unique and isolated a population must be before it is a "stock." Intraspecific structure theoretically can range from complete panmixia (no intraspecific structure) to isolation so complete for so long that speciation processes are at work or almost complete (Fig. 1). Rather than a universal definition that could be applied in the regulatory arena to decide if a population is or is not a "stock," what is required (and more practical) is a means of describing the usually complex biological population structure in a more informative manner.

The purposes of this paper are to show that currently used simplistic definitions of stocks are not very useful in satisfying management objectives and to suggest a way to describe population structure that captures its complexity. Using examples from the marine mammal and fishery literature, we review the history of the stock concept and methods currently used to infer stock structure. We suggest how to classify the various qualities of stocks and conclude with a case study demonstrating how the suggested method can be applied.

Background

Around the turn of the century, pioneering fishery biologists F. Heincke and J. Hjort established the local self-sustaining population as opposed to the typologically defined species as the preferred unit of study for fisher-
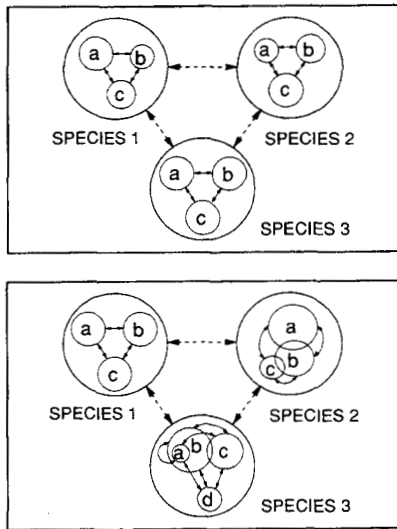
TWO VIEWS OF INTRA-SPECIFIC STRUCTURE

Figure 1. Two views of intraspecific structure, a "typological" and a "biological" conception of populations within species. The circles, labeled with lowercase letters, are individual populations whose geographical habitat is represented by its size and position within the species space. Where circles intersect, habitat is shared. The arrows represent exchange rates: infinitesimal between species, variable between populations within species.

In the first view, individual populations within a species are perceived as isolated, allopatric entities that can be uniquely described. Interchange between the populations, while greater than between species, is still very low, on the order of a few genomes per generation.

In the second view, the complexity and wide range of potential intraspecific structures are recognized. Habitats range from completely separate to situations where one is completely within another. Exchange rates vary between various populations, in some cases with great temporal variability due to environmental and population density changes.

ies-management questions (see Sinclair 1988; Gauldie 1991). Independently, Leopold (1933) recommended managing populations of wildlife based on their "radius of mobility," "rate of spread into unoccupied range," and "minimum units of range and population." This basic approach of managing a species at some subspecific level has therefore been a tenet in resource management for almost 100 years. In general, stock status is

conferred using a variety of proxies that imply reproductive isolation. With isolation comes genetic divergence through drift and through local adaptation via processes such as differential selection or character displacement. But because reproductive barriers within species are fragile or incomplete, especially in the marine environment, the degree of isolation of one population relative to others can be complex, varying both in space and time.

A variety of other terms in the literature all refer to organizational levels below the species: subspecies, race, deme, stock, and management unit. The use of such terms in resource management literature is highly inconsistent. Only the term "subspecies" is recognized by the International Code of Zoological Nomenclature; it is applied to populations that have received a trinomial name. The other terms, lacking such accepted usage, are frequently used to describe a variety of populations for analytical convenience or to provide status to a group because that is the most conservative approach when data are lacking and conservation issues predominate. Many so-called stocks are mere "ecological abstractions" (Sinclair 1988), and a perusal of the management literature indicates that when a term such as "stock" is used, it is used in the simplest and least restrictive sense. Little qualification is made or assumed about its genetic, evolutionary, or ecological implications. Misconceptions occur later when such stocks are expected to behave as if they were biological populations.

In 1980, an ambitious attempt to formalize the stock concept was made with an international symposium (Stock Concept International Symposium convened at Alliston, Ontario, September 29–October 9, 1980; see Booke [1981] for proceedings citation). Although many speakers emphasized the importance of management by stock, in that very large symposium only one author ventured any formal definitions. Booke (1981) defined a "phenotypic stock" as any population that maintains characteristics that are expressed depending on the environment, and a "genotypic stock" as a population maintaining Hardy-Weinberg equilibrium, that is, constant gene frequencies for a particular character in each generation. The definition of phenotypic stock is similar to a later definition by Brown et al. (1987): a population whose average life history parameters are meaningful from the standpoint of management. The definition of genotypic stock is similar to the definition of Larkin (1972), who described a stock as a population having a degree of genetic uniqueness: "a population of organisms which, sharing a common environment and participating in a common gene pool, is sufficiently discrete to warrant consideration as a self-perpetuating system which can be managed" (p. 11). Hoelzel and Dover (1989) defined a genetic stock as one that is genetically

differentiated. Presumably the genetic stock is the population that Sinclair (1988) called the "local population" in his essay on population regulation and speciation. Recently, Gauldie (1991) published a thorough review of stock concepts and their deficiencies as applied to exploited fish populations and argued for a model of populations defined on the basis of degree of interchange.

This sense of biological uniqueness via isolation is an evolutionary one, because it acknowledges the population's adaptation to local conditions and indicates that it possesses a reservoir of unique genetic variability. This is the "evolutionarily significant unit" (ESU) (Ryder 1986; see Waples 1991 for a review of its application to northwestern salmonid stocks); it is a biological population that is distinguished by its presumed evolutionary uniqueness and significance. It is a natural unit and should be a better management unit than an unnatural unit (Sinclair 1988).

Few would argue with this reasoning. In practice, however, it is difficult to define a stock based upon principles of adaptive genetic uniqueness. Existing measures of fitness are of little use in defining specific adaptation to a local environment; experimentally this is an intractable problem for higher animals. As a result, stocks are typically defined using a variety of proxies that suggest this adapted genetic uniqueness.

Stock Criteria

To study stock structure, an investigator makes observations of allopatry or isolation that imply reproductive isolation; differential life history responses, which also imply reproductive isolation; morphological (i.e., protein structures) differentiation, indicating drift or evolution under different selective regimes; or differentiation of neutral genetic characters quantifying the degree of isolation and the time since an ancestor was shared. We have categorized these sources of information as (a) distributional, (b) population response, (c) phenotypic, and (d) genotypic.

Distributional Data

Initially the most important items of knowledge are those of distribution and abundance. These data pertain to all aspects of abundance, migration, pollutant and parasite loads, zones of fishery interaction and conflict, etc., that provide information about the population movements relative to geographical space and time. These data largely define whether there are major geographical barriers between putative stocks and whether they are allopatric, parapatric, or sympatric.

At the most basic level and without additional information, disjunct populations frequently have been designated as separate stocks for management purposes (e.g., Perrin et al. 1985). This is certainly a conservative

approach. Even populations that overlap for portions of their life cycle may be disjunct stocks (Iles & Sinclair 1982). Overlapping distribution does not necessarily imply gene flow; natural processes favoring adaptation to local conditions, or social selection favoring maintenance of local social behaviors, especially in the case of marine mammals, may preserve genetic differentiation in the face of apparent overlap or movements between populations (Ehrlich & Raven 1969; Slatkin 1987; Baker et al. 1990).

Presence and absence data on distribution are the most readily available sources of information on which to base stock identification decisions, but they may be misinterpreted when search effort is not continuous, causing artificial discontinuities in the reported distribution. Abundance information provides a better proxy for exchange rates. Density "troughs" or large areas of zero density indicate extrinsic barriers. Unfortunately, the variability associated with most estimates of density is such that the statistical power of using differences in density gradients in assigning stock status is often low.

Because of the importance of reproductive isolation in speciation, information on the physical movement of individuals (telemetry studies, mark-and-recapture, etc.) within their ranges brings one closer to properly assigning stock status to populations. Reeb and Avise (1990) and Avise and Ball (1990) described evidence of concordance of genetic patterns with movements for a variety of species in response to biogeographic barriers. Thus, for most populations, research on movement patterns should be given high priority.

Population Response Data

Although used frequently to distinguish putative populations, a population's life histories and behavioral traits may be modified by the environment through density-dependent control mechanisms. Data include all aspects of demography (age at sexual maturity, fecundity, growth rate, and mortality), other biological parameters, social behavior, vocalization, and specific interactions peculiar to a particular population. Behavioral characteristics are probably modified by exploitation and intra- and interspecies competition, which affect breeding site fidelity, nursing and care-giving to the young, and feeding habits, which in turn affect the pollutant and parasite loads. Still, an advantage to using population response criteria over abundance criteria should be recognized: Samples taken at one point in time when population response criteria are used integrate movement patterns over a much greater time scale than do abundance criteria.

Differences in the timing of breeding provide a particularly valuable criterion, because they imply that a barrier exists to gene flow between populations. A stock division of spotted dolphins (*Stenella attenuata*) in the

eastern tropical Pacific, for example, was originally based entirely on distribution and morphology (Perrin et al. 1979), but later was supported by differences in reproductive parameters (Barlow 1984, 1985).

Phenotypic Data

The concept of self-sustaining stocks was formulated by Heincke through his extensive examination of discontinuous geographic variation in Atlantic herring morphology (Sinclair 1988). Stocks have been defined by morphological differences of every type: color patterns, body size, shape, and skeletal characters are some examples. (Electrophoretically detectable differences in proteins are treated as genetic characters if there is evidence that such differences are inherited.) For homeotherms, morphological differences probably represent underlying genetic differences, and analyses of DNA and morphology should provide similar evidence regarding phylogenetic structuring of other groups (Sytsma 1990). The relative morphological differences between populations can be assumed to be a record of past (or present) differences in selection pressures or genetic drift. However, there are instances where morphological and molecular evidence differ due to either methodological or actual biological problems (see Box 1, Sytsma 1990). For instance, differential migration between sexes might produce strong mtDNA differences but little difference in chromosomal markers if males stray between populations and females do not. Some morphological patterns, possibly color patterns or size differences, may be ecophenotypic, that is, not stable to environmental variation. However, differences in morphological characters in mammals and birds usually yield clear information regarding population uniqueness; because the variation is assumed to be both adaptive and heritable, it is a record of past selection pressures. Given adequate sampling, morphological differences between two or more populations strongly suggest limited gene flow among these populations due either to extrinsic barriers or selection. Like the population response criteria, these types of phenotypic data integrate movement patterns over a much larger time scale than do abundance data.

Morphological differentiation has been the predominant reason for assigning stock structure to marine mammal populations. Perrin et al. (1985), for example, documented population-specific differences for spinner, spotted, and common dolphins (*Delphinus delphis*) in the eastern tropical Pacific; stock status and mortality quotas have been applied to the take of those populations by U.S. tuna purse-seiners (Anonymous 1987). Roest (1976), and more recently Wilson et al. (1990), used skull morphology to separate sea otters from Alaskan and Californian waters into separate stocks subsequently used as management units.

Genotypic Data

Booke (1981) defines a genotypic stock as a random mating population maintaining Hardy-Weinberg equilibrium; presumably, it can be defined as any random mating population that shows fixed genetic or temporally stable gene frequency differences when compared to other populations. Data include those from all studies that involve the analysis of some part of the genotype. The studies can be classified into analysis of proteins via isozyme electrophoresis or immunological techniques, molecular cytogenetics, and analysis of DNA by DNA-DNA hybridization, restriction site analysis, and sequence analysis (see Hillis & Moritz 1990 for a thorough review). The techniques involved in genetic studies and their application to marine mammals have been reviewed recently by Hoelzel and Dover (1989) and have been the subject of a recent International Whaling Commission workshop (Hoelzel 1991).

The evidence obtained from genetic methods is considered by resource managers as the most unequivocal for differentiating species and their intraspecific structure. Using genetic information for management purposes presents problems, however. Clearly it could be the ideal tool if we could directly examine the genes that constitute the locally adapted genome. One cannot do this and must rely on the analysis of "neutral" genes, primarily using allozymes and mtDNA, that are assumed to be mostly independent of selective forces. If this assumption can be made and if complete isolation if assumed, the degree of genetic divergence between two populations is a measure of the relative time since they shared a common ancestor. While we believe that significant morphological differences usually represent adaptive evolution in disparate environments, mtDNA differences between two populations may simply be a measure of time of separation. Rapid evolution through drift could accumulate significant mtDNA differences in different allopatric populations that inhabit similar environments. Still, none of these populations would presumably harbor unique adaptive genetic variability and would perhaps not warrant separate management status. In the opposite situation, lack of significant mtDNA differentiation between two populations does not necessarily mean that stocks are separate. Where barriers are "leaky," mtDNA genomes can rapidly penetrate neighboring populations independent of the adaptive chromosomal genome (Ferris et al. 1983). These "foreign" mtDNA genomes are not selectively removed from the population—they are presumably neutral. The appearance of these foreign genomes may argue for the presence of "homogenizing" gene flow and lumping the populations as one stock. In actuality, significant variation between the populations still may develop in the chromosomal genome due to differential selection pressures. As an extreme example, in Lake Victoria, 14 mor-

phological species representing 9 genera of chiclids show almost no differentiation in mtDNA sequences that are 803 base pairs in length (Meyer et al. 1990). In this case mtDNA would be a poor proxy for demonstrating differences in adaptive variation between populations.

In fact, most past genetic studies of marine mammals and other pelagic animals were not very useful for management purposes. When significant gene frequency differences between two putative populations were not found, it was easy to pass off the result as a negative one (i.e., the test was insufficiently sensitive because not enough samples or polymorphic loci were tested). And when significant gene frequency differences were detected among populations, the resource biologists have probably known from a variety of other criteria that gene flow among the groups was highly restricted. This is because considerable time and isolation were required to generate detectable differences, that is, no more than a few individuals per generation. Resource managers, however, divide populations into separate units when interchange rates are as much as several percent per year.

However, sequencing progressively longer segments of the mtDNA and nuclear genome now offers means of detecting genetic differentiation in the face of exchange rates that may be considerably higher than a few genomes per generation moving between the populations. After all, at some level, all genomes are different. So now one must ask what level of differentiation or gene flow indicates that a population has become "pan-mixed"? Deciding this requires an understanding of how much gene flow and consequent genetic diversity is "significant" or not.

Phylogeographic Taxa

Clearly, the complex interactions among movement, introgression, and selection of nuclear and cytoplasmic genomes (and the variability of expression of those genomes between local populations of a species) result in situations that are not conducive to a simplistic definition of stock or a binomial decision of stock or not-stock. Deciding whether a putative local population should be managed as a separate unit requires considerable expert biological judgment. As long as there are no means of routinely measuring the *total genetic variability of local adaptation*, rather than its proxies (distribution, population responses, phenotypic variation, or neutral genotypic variation), quasisubjective decisions are necessary.

For other purposes, Avise et al. (1987; Avise 1989) devised a framework for organizing hypothetical population structures and relating the two critical concepts

of selection and movement or their products— phylogeny and distribution. They first proposed five categories but later reduced them to four (Avise 1989), two with discontinuous genetic patterns and two with continuous ones. The approach classified assemblages into one of four categories based on two criteria: mtDNA genetic distance and spatial distribution. In a recent publication, Avise and Ball (1990) characterize the interaction of both extrinsic and intrinsic reproductive barriers in the formation of subspecific divisions and emphasize the surrogate nature of most genetic and other measures (which we call proxies) of so-called stock distinctiveness.

We altered their original catagory criteria slightly to be more general and to emphasize that meaningful distinctiveness must come from the expression of multiple, independent genetically based traits (Avise & Ball, 1990). *In our alteration, the horizontal axis indicates the degree of response to differential selection likely to have occurred in one population relative to another.* It represents differences in characters that are the expression of the locally adapted genome, rather than simply the mtDNA genetic distance (Fig. 2). Under this scheme, differences found in demographic, morphological, isozyme, or mtDNA measures are taken to be proxies indicating that selection may be operating differentially

Theoretical classification:

		PHYLOGEOGRAPHIC TYPES	
GENE FLOW	little or none	III	I
	high	IV	II
		little	great
		DIFFERENTIAL SELECTION	

Operational classification:

		PHYLOGEOGRAPHIC TYPES	
GEOGRAPHIC LOCALIZATION	great	III	I
	little or none	IV	II
		little	great
		PROXIES for DIFFERENTIAL SELECTION	

Figure 2. Four phylogeographic classification categories. The horizontal axes in the theoretical classification refer to differences in the characters expressed by the genes that make up the locally adapted genome. The horizontal axis in the operational classification refers to differences in characters that may or may not be expressed by the genes that make up the locally adapted genome. If they are not expressed, the differences represent proxy measurements indicating the probability that sufficient time has elapsed and selection pressure has been applied so that a locally adapted genome has evolved. Gene flow is defined as production of locally fit offspring. Adapted from Avise (1989).

on one population relative to another. Measures on this axis mostly represent the culmination of selection operating on many generations.

The proxy for gene flow, distribution difference, is the other axis of the matrix. It is considered separately to emphasize that available information usually only indicates potential gene flow. Actual flow of genes requires the production of fit offspring. The advantage of looking at populations in this way is that a matrix of four population relationships can be *operationally* described. It is a hierarchical organization because with each step there is an increasing *probability* of the population in question being an ESU (Phylogeographic categories I through IV; Fig. 2). Note that a stock is always characterized as a "population" in relation to another reference population. The proposed system works as follows:

Category I Populations

The easiest situation to deal with is that of allopatric populations demonstrating significant genetic differences; there would be little argument that these should be managed as separate units. Category I is characterized by a discontinuous genetic divergence pattern where locally adapted and closely related genome assemblages are separated from others geographically and by significant genetic distances—great genetic divergence/strong geographic partitioning. This could have been caused by long-term, extrinsic barriers (zoogeographic) or by extinction of intermediate assemblages in cases with limited gene flow.

Category I situations are characterized by the presence of actual geographical separation by physical barriers such as land masses, or oceanographic or topographical barriers such as temperature clines, etc., which effectively create a margin around a population. Genetic and other differences from populations elsewhere are implied but are not necessarily proven. The population is effectively isolated and probably is never confused with another in management programs.

Category II Populations

Category II is characterized by a discontinuous genetic diversity pattern between groups of closely related genome assemblages existing sympatrically or parapatrically—that is, great genetic divergence accompanied by weak geographic partitioning. Avise et al. (1987) speculate that this may have arisen through allopatric divergence and secondary contact or through some intrinsic (reproductive) barriers.

This requires that two (or more) populations/putative stocks coexist with total sympatry or with extensive geographical overlap or be weakly defined in parapatry. Geographically there would appear to be no reason not

to manage them together, but critical differences in behavior, morphology, genetics, or some combination of these indicate reproductive isolation to some degree. This type of stock is perhaps the most critical and difficult to manage.

Avise et al. (1987) and Avise (1989) find no good examples of this category and report that it is rare to find mtDNA differences greater than 1 to 2% between individuals collected from the same locality. Using mtDNA divergence measurements, Hoelzel (1991) reports considerable genetic isolation between at least partially sympatric populations of killer whales (*Orca orcinus*) off Vancouver Island; they suggest that these groups represent a category II population structure. They are not category I (or III) populations because of their at least partially sympatric distribution and potential for genetic interchange.

Category III Populations

The remaining two categories are characterized by a pattern of continuous genetic divergence. Category III parallels category I; however, here the geographically separated assemblages are characterized by little genetic differentiation, for instance, less than 1% for mtDNA diversity. Still, the populations are clearly separate, either because of true allopatry or strict parapatry, and there is a high degree of reproductive isolation, as evidenced by various combinations of demographic and morphological differences, although there are no barriers to intermingling at the margins and interbreeding is feasible. There may or may not be various combinations of demographic, morphological, and genetic differences. In any case, geographically concordant unique genome assemblages have developed within local habitats in response to local selection pressures.

Category IV Populations

Category IV populations have extensive gene interchange and no subdivision by geographic barriers. Populations in this category appear panmictic and occupy a broad range that blends with that of neighboring population(s) rather than abuting on them. There are usually minimal, if any, differences in morphology, genetics, and demographic parameters between them, and the main distinguishing feature indicating that this is a separate population is that the center of abundance may be some distance from the center of neighbors. There is little or no reproductive isolation, and there is considerable intermingling on the breeding grounds. This category typifies the most nebulous classification and may show poor evidence for any stock differentiation. Depending on the management issue, certain geographical regions occupied by such populations may still be treated as separate stocks for the sake of conservatism.

Qualified Phylogeographic Taxa

The manner in which such a phylogeographic classification of any given population is made and the confidence in such a decision depends on the amount of information available. We suggest that this information be appended to the phylogeographic taxa using a shorthand method (Fig. 3). A shorthand notation is necessary because resource management documents usually contain extensive lists of stocks that have received or are being considered for separate management status. Using this approach, reference to a given management unit would carry with it information regarding its phylogeographic structure (category type) and the data from which the decision was made (criteria basis).

The phylogeographic category is designated by a Roman numeral (I, II, III, and IV; Fig. 2). The proxy information with which decisions regarding the population are made is designated as "a" (distribution and movement), "b" (population responses), "c" (phenotypic differences), and "d" (genotypic differences). A population would be designated by phylogeographic category and decision criteria, for example, II a/bcd. Letters to the left of the solidus represent data for "lumping" and those to the right, data for "splitting" the group (Fig. 3).

A population that has a high probability of being an ESU is immediately apparent from its phylogeographic category. The degree of confidence in such a classification is indicated from the type of information that was marshalled to make the decision. Situations where information was lacking or equivocal could be informative from a management sense. In cases where information regarding one or more of the criteria was unavailable, the letter designation would not be present (perhaps a dash could be substituted), or the same letter could appear on both sides of the solidus if information was equivocal or unresolvably contradictory. A stock designation of type III c/ad would probably stimulate more

aggressive management than one designated as III c/a, and such a designation would help focus additional research efforts. Where there is clear geographic separation but extensive overlap of margins temporally, as in type III, we might wish to denote this fact by indicating the stock as III a/a. In another example, where population response is to be included in the stock criteria, there might be no difference between demographic parameters and pollutant and parasite loads, but clear differentiation between dialects. The stock that perhaps might be type II might then be designated as II b/b. If all aspects showed clear differences, then the category would be II /b.

In the appendix, we have chosen a marine mammal species to illustrate the procedure. The minke whale (*Balaenoptera acutorostrata*) has populations with relationships demonstrating each of the four phylogeographic categories. Current biological information on the minke whale is provided in detail, covering as much ground as possible under each of the four criteria. Classifications are suggested for the various putative stocks.

The Decision Process

This proposed system of phylogeographic classification of course addresses only single-species considerations. Because of ecological phenomena such as predator-prey interactions, the existence of keystone species and species guilds, etc., a population may be important beyond its qualifications, or lack thereof, as an ESU; these factors must also be considered in deciding what should comprise a management unit.

It is most important that the phylogenetic classification be carried out as an exercise separate from and prior to consideration of the socioeconomic and political factors that inevitably influence the management status of a population, and, further, potential conflicts of
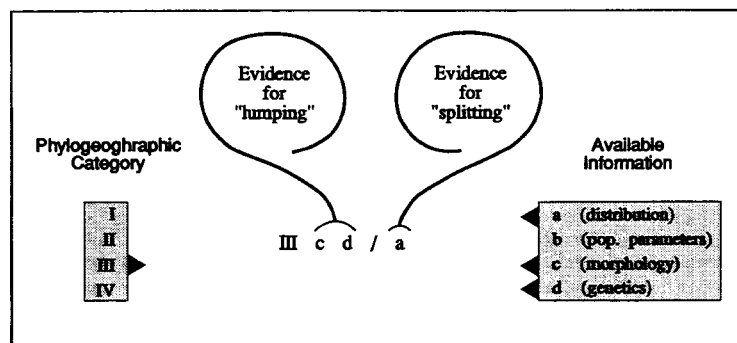

Figure 3. A shorthand method for qualifying stock type using phylogeographic categories and information regarding the criteria used to make such qualifications.

interest should be carefully weighed and considered in selecting an expert or panel of experts to make the classification. Ideally, populations should be surveyed and phylogeographically classified *before* situations demanding management decisions arise.

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Appendix

In the earlier part of this paper, we endeavored to show how stocks may be classified, with the aid of some guidelines, into one of four major categories. Information that describes characteristics of populations may then be added as qualifiers to include (a) distribution, (b) population response (demographic or behavioral), (c) phenotypic information (morphologic), and (d) genotypic information (Fig. 3). Arguments for classification must be made in the knowledge that information is constantly being updated and that intraspecific populations themselves are dynamic and therefore subject to change over time and in response to new information. Our attempts at classifications are thus open to testing both now and in the future.

Minke Whale

Balaenoptera acutorostrata

I. Taxonomy
  A. Subspecies—*bonaerensis*
  B. Morphs
    1. Davidsoni-type
    2. Bonaerensis-type
    3. Dwarf
II. Provisional management units*
  A. Southern Hemisphere—six management areas defined by longitude from the equator to ice edge
    1. Area I, 120°W–60°W
    2. Area II, 60°W–0°
    3. Area III, 0°–70°E
    4. Area IV, 70°E–130°E
    5. Area V, 130°E–170°W
    6. Area VI, 170°W–120°W
  B. Northern Hemisphere—two main populations, one smaller
    1. North Atlantic
      a. Canadian east coast
      b. Central

      c. West Greenland
      d. Northeastern
    2. North Pacific
      a. Okhotsk Sea—Western Pacific
      b. Sea of Japan—Yellow Sea/East China Sea
      c. East Okhotsk Sea—Western Pacific
    3. Northern Indian Ocean
III. Evidence
  A. Distribution
    1. Range

Distribution is global, but there is no evidence from tagging, abundance, etc., that Northern and Southern Hemisphere populations mingle at any time, even though the equator may be breached in some regions, for example, off Brazil. The pattern of latitudinal seasonal migration associated with feeding (in polar waters) and breeding (in warm low latitudes) effectively isolates the populations of the two hemispheres, which are out of phase by 6 months. However, there is a possibility, yet to be proved, for interchange in some marginal equatorial regions where temporarily segregated portions of the population such as mature females or males may reside almost year-round. Latitudinal segregation of different portions of the population by sex, age, and reproductive status are well documented (Wada 1989).

Tag return data suggest mixing longitudinally at the boundaries (as defined above) between southern stocks (Wada 1984). There is evidence for interchange between Areas IV and V, for example. The region of occupation of the dwarf form in the southern oceans is longitudinally wide (Southwest and Southeast Atlantic, Southwest Pacific), but it is perhaps excluded from high latitudes (Best 1985; Arnold et al. 1987).

In the Northern Hemisphere, stocks have been defined mainly in response to national and regional exploitation patterns and to a large extent were originally not biologically based. Tag experiments do not link West Greenland animals with the eastern Atlantic ones, and they appear to be separate. The species is highly migratory, and movements of several thousands of kilometers, even within a few days, are well documented in latitudinal direction (Horwood 1990). Unless there are actual or partial geographic, oceanographic, or other barriers to east-west excursions, the whales from the various regions must be considered to probably intermingle.

The relationships of the minke whales in the southern and northern Indian Ocean are not known, although populations exist on each side of the equator. The southern animals clearly occur in and around Areas III and IV. In the northern region, animals are observed year-round in the Red Sea, Gulf of Aden, Persian Gulf, and the seas surrounding Sri Lanka and Indonesia (Horwood 1990).
    2. Contaminants

Tanabe et al. (1986) reported concentrations of PCBs (0.0031–0.029 ppm wet weight) and DDEs (0.013–0.14

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ppm wet weight) in blubber of Antarctic Area IV and V minke whales to be mostly lower than those observed for the Northern Hemisphere, where levels are 0.14–1.1 ppm wet weight for PCBs and 0.21–2.6 ppm DDT off West Greenland (Johansen et al. 1980), and 27.45 ppm PCBs and 1.09 ppm DDT in the St. Lawrence estuary, Canada (Sergeant 1980). The differences are clearly due to feeding ground separation, and show clear distinctions between the hemispheres.

3. Parasites

Comparison of infestation rates of ectoparasites in adjacent Antarctic Areas I, II, and III (Bushuev 1986, 1988) suggest that differences exist between populations. In Area III, 34–57% of the whales are infested, compared with 2–11% in Area II (with variable incidence from east to west) and almost zero infestation in Area I. Ohsumi et al. (1970) reported very low ectoparasite infestation in Area IV, and later investigation over 3 years showed significant differences between Areas I, III, and IV. The differences were interpreted as indicating that stocks are separated on the feeding grounds.

B. Population response

The Southern Hemisphere minke whales have been documented to respond indirectly to exploitation of competitor species in a density-dependent manner, with consequent reduction in the age at sexual maturation from about 12–13 years to 7–8 years during a 30-year period (Area III) (Kato 1987). Masaki (1978, 1979), Kato (1983), Kato et al. (1984), and Ohsumi (1986) reported similar changes in age at sexual maturation for Areas III and IV combined. The pattern of trends and values of biological parameters seems similar for the Areas, but perhaps the response has been greatest in the most heavily exploited Areas, I, II, and III (Horwood 1990).

Rather less is known for the Northern Hemisphere because of difficulties in age determination. Still, sexual maturation is reported to be about 7.3 years in the North Atlantic.

C. Phenotypic Data

The Northern and Southern Hemisphere forms of the minke whale are different in coloration (flippers, baleen, etc.) size, and skeletal morphology, the southern form being designated as the *bonaerensis* form. With the exception of the newly described dwarf form, mature animals from the southern population are generally larger than those from the northern populations (Lockyer 1984). The Atlantic minke is also slightly larger than the Pacific minke.

In the Southern Hemisphere, two morphological types were traditionally reported, one with plainly pigmented flippers and the other with asymmetrical two-tone coloration; both belong to the *bonaerensis* form (Williamson 1959; Ohsumi et al. 1970; Taylor 1957; Aguayo 1974; Baker 1983; Gaskin 1972; Kasuya & Ichi-

hara 1965). Currently, there are three reported color forms of minke whale, mainly defined on the basis of extent and symmetry (left and right sides) of flipper coloration—the presence, absence, or intermediary of a white band, the extent of pale coloration of the baleen, and dark pigmentation around the neck and throat region (Best 1985). The new evidence for a diminutive or dwarf form in the southern oceans, mainly reported from South Africa, Australia, New Zealand, and Brazil (Best 1985), is largely based on the definition of a third color morph characterized by symmetry of coloration and white flippers. In addition, the third form is consistently smaller. Best (1985) concluded that the dwarf form was also sufficiently different in skull characters from the southern *bonaerensis* subspecies that it was at least as distinct as the northern *davidsoni* form from the *bonaerensis* one.

D. Genotypic Data

Restriction fragment analyses using 14 restriction enzymes of minke whale mtDNA D-loop from four populations—Antarctic Areas IV and V, *bonaerensis* type, Antarctic Area IV dwarf form, Sea of Japan and western North Pacific (*davidsoni* type)—indicated 4–11% genetic nucleotide diversity (Wada et al. 1991). In Areas IV and V (*bonaerensis* form) the genetic diversity within populations is only 0.17%, compared with 0.05% within the western North Pacific and 0.00% within the Sea of Japan. Nucleotide diversity shows no significant differences between Areas IV and V, but significant differences between the *bonaerensis*, dwarf, and *davidsoni* forms, the latter two being relatively more closely related, with genetic diversity of about 4% (Fig. 4).

The diversity between the Sea of Japan and the western North Pacific is only 0.06%, but is >10% between Northern and Southern Hemisphere minke populations. Wada and Numachi (1991) presented results of enzyme electrophoresis on tissue proteins from different balaenopterid whales that indicated that genetic differentiation between Antarctic and western North Pacific Sea of Japan and Korean stocks was about seven times
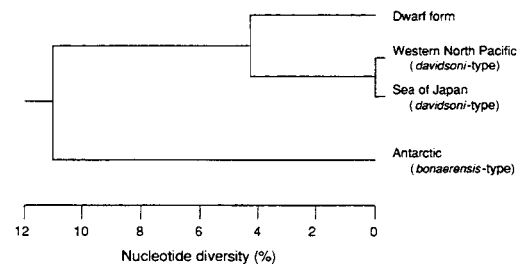

Figure 4. mtDNA sequence divergence among four minke whale samples. After Wada et al. (1991).

greater (D = 0.0826) than that within the North Pacific, to the extent that the differences were far greater than those between the separate sibling species *B. borealis* (sei) and *B. bryde* (Bryde's). This suggested that northern and southern minkes were separate species, or at least separate subspecies.

DNA nuclear probes suggest significant differences between the Antarctic, North Atlantic (West Greenland), and the western North Pacific (Sea of Japan) populations (Amos & Dover 1991). The results could be translated into migration rates between regions. The high level of migration between adjacent Areas IV and V was enough to make separate stock identity questionable (Hoelzel & Dover 1991).

In the North Atlantic, Palsboll (1990) reported on restriction fragment analysis of ribosomal DNA of minkes from the Northeastern Atlantic (Barents Sea) and West Greenland. He found that there was a probability of less than 0.001 that the two stocks were from a single random-mating population—good reason for identifying the stocks as separate. Arnason and Spilliaert (1990) reported evidence of stock differences between minkes from the Norway (Northeastern stock—Barents Sea), Iceland (Central stock), and West Greenland. Using genomic DNA probes, they found the greatest differences between West Greenland and the others. Differences were also found between Iceland and the Barents Sea populations. They concluded that existing management stock divisions were valid. Danielsdottir et al. (1990) also found supporting evidence using electrophoretic analyses on the separation of these three stocks. Using restriction fragment analysis of mtDNA, however, Palsboll (1990) found conflicting and contradictory results for these three regions. Bakke and El-Gewely (1990) reported stock differences between northern Norway and the west coast of Svalbard using the same techniques.

IV. Classification

The minke whale has been comparatively well investigated and defined in terms of stock identity, probably because the species has been exploited on an international scale. The evidence seems strong that the Northern and Southern Hemisphere populations are clearly distinct and in category I b/abcd status, and the subspecies category seems valid. The North Atlantic and North Pacific stocks also appear distinct and in category I status.

In the Southern Hemisphere, clearly it seems that populations in Areas III, IV, and V are not easily discernable and probably should be afforded category IV abcd/a status—very weak stock definition, if any. However, compared to the southern *bonaerensis* subspecies, the dwarf form also could be afforded subspecies status, but it would be ascribed to category II because of sympatric distribution. The final categorization might be II a/cd.

The North Atlantic stock definitions appear to be largely supported by genetic analyses, and the majority when compared would be given category III c/acd status.

This species is of particular interest in stock analysis because of multiple representations in each stock category, I–IV. The recent genetic investigations have brought to light the fact that speciation, not just subspeciation, may be occurring in the minke whale populations. In the future, the whole question of what constitutes a species may have to be reconsidered for the family Balaenopteridae.

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