



## Forward

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### Marine mammal subspecies in the age of genetics: Introductory remarks from the Associate Editor and Editor-in-Chief of *Marine Mammal Science*

**MICHAEL K. SCHWARTZ**,<sup>1</sup> Associate Editor, *Marine Mammal Science*, National Genomics Center for Wildlife and Fish Conservation, U.S. Forest Service, 800 East Beckwith Avenue, Missoula, Montana 59801, U.S.A.; **DARYL J. BONESS**, Editor-in-Chief, *Marine Mammal Science*, Center for Excellence in the Marine Sciences, University of New England, % 41 Green Acres Road, Hartford, Maine 04220, U.S.A.

Almost every conservation genetics and evolutionary biology textbook has a section questioning: “What is a species or subspecies?” It has been one of the most discussed, nearly unanswerable questions in all of biology. At issue is how to logically divide a variable that is generally continuous, with some occasional discrete breaks. Answering this question is at times akin to addressing the questions: “How many colors are in a rainbow?” or “Where does red end and orange begin?” School children can tell the two colors apart at the middle part of their defined range, but defining the color of light at 589 nm (the arbitrary boundary between the colors) may be as much about the observer, their perceptual rules, and their experiences as it is about the physical experience of seeing a specific wavelength.

How one defines a species is influenced by the concept of species, the tools used to evaluate that concept, and by scientific experience. Defining a species has historically conflated the philosophical and theoretical concepts of what a species is with the pragmatic and methodological problems of species delimitation (Mayden 1997, de Queiroz 2005). De Queiroz (2007) has argued that most species concepts share the common element that species are segments of separately evolving metapopulation lineages. Differences arise in the lines of evidence used to evaluate the evolutionary history and trajectory of each lineage.

As segments of a metapopulation lineage journey on their own trajectory from other segments they accumulate changes. These changes can be in the genome or in morphological, behavioral, physiological, reproductive, or other biological traits of the species. Yet, these changes do not occur in the same sequential order, or at the

<sup>1</sup>Corresponding author (e-mail: michaelkschwartz@fs.fed.us).

same rate during the speciation process. Changes in the genome (*e.g.*, substitutions) may occur before there is any discernible morphological change. For example, neutral substitutions do not create functional differences, although they can act like a clock recording time since populations last were connected. Alternatively, one or few gene substitutions of large effect may quickly render individuals reproductively incompatible (Nosil and Schluter 2011). To complicate matters, genetic change does not always come before other types of changes in a population. If the species is plastic in its response to the environment, behavioral or morphological change may precede genetic change (Crozier and Hutchings 2014, Sgrò *et al.* 2016). The asynchrony and unpredictability in the sequence of biological change during evolution makes defining species with a concrete set of rules complicated.

Species concepts are often distinguished by the relative weight placed on what is different (or not different) between species. The Biological Species Concept (BSC) defines species as “a group of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups” (Mayr 1942). Here, weight is placed on reproduction. This is a logical choice as reproductive incompatibility leads to population divergence. The problem is many populations can separate into species despite ongoing interbreeding and gene flow (Hausdorf 2011). The Phylogenetic Species Concept (PSC) places weight on ancestry over morphology or behavioral differences. It suggests that a species “. . . is a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind” (Eldredge and Cracraft 1980). However, historical and contemporary hybridization between well recognized morphological species (*e.g.*, brown bears and polar bears) can cloud the pattern of ancestry limiting efficacy of ancestry alone to define species. Alternatively, the PSC can artificially create new species if species distributions are fragmented and each fragment becomes fixed for different DNA polymorphisms through the neutral process of genetic drift and not through local adaptation. Overall, this shows the complexity of leaning on one set of rules or characters to define species. Other species concepts, such as the ecological species concept, the genotypic cluster, or the evolutionary species concept exist because of the greater weight placed on one component over another of the biology of an organism (Simpson 1951, Van Valen 1976, Mallet 1995).

Added to the complexity of species concepts is the fact that scientists are “conflicted investigators” (Hey 2001). As humans we are not inherently objective nor do we have uniform perceptions. Scientists work with specific taxa that have distinct evolutionary patterns and scientists often have expertise with specialized tools. These experiences influence perception and perhaps how one defines a species. For example, the BSC, largely applicable for use with biparental organisms, was proposed by Earnst Mayr (Mayr 1942). It is no coincidence that in addition to being an evolutionary biologist Mayr was an ornithologist. It is unlikely that he would have derived the BSC if he was a mycologist or microbiologist. Similarly, the PSC may be more readily adopted by scientists studying mammals over plants, because hybridization in mammals is less common than in plants.

If defining and delimiting species is complex, defining subspecies is tortuous. Charles Darwin (1859) recognized the problems with defining units below species when he wrote: “No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species. . . The term ‘variety’ is almost equally difficult to define; but here community of descent is almost universally implied, though it can rarely be proved.” For Darwin a variety was

taxonomically lower than a species. They are entities that progressively transmuted into species (Ereshefsky 1992), but were vague and messy during this transformation.

Those working for natural resource agencies in a management, regulatory, or scientific capacity recognize the challenges of defining units at and below the species level, but do not have the luxury of ignoring these challenges. If entities below the species level are eligible for protection under a legal framework, then it becomes critical to define them. The U.S. Endangered Species Act (1973) considers any subspecies of fish or wildlife or any distinct population segment an entity available for protection. The Marine Mammal Protection Act (1972) also looks to protect entities below the species level, called population stocks. Taylor *et al.* (2017*b*) note that unnamed taxa are unlikely to obtain equal protection compared to named taxa. If these cryptic entities are not identified, their options for legal protection are limited. It would seem ethically corrupt to push a taxon, such as a subspecies or stock, to extinction before we even knew it existed.

Despite all the complications in defining subspecies, the legal need to do so has become essential. Scientists must work to make sure that guidelines (data to include and analyses to conduct) and quantitative standards (the magnitude of differentiation expected at different taxonomic levels) used to delineate taxa, especially below the species level, are based on best scientific practices. Articulating guidelines and standards provides transparency to the public and decision makers, while informing future sample collection and study. This special issue of *Marine Mammal Science* focuses on guidelines and quantitative standards for the use of molecular genetic information in delimiting species and subspecies of cetaceans. It is led by scientists working throughout the National Marine Fisheries Service who aim to provide an evolving document for advancing the management and protection of cetaceans. It will hopefully serve as a model for others with different technical expertise (*e.g.*, ecologists, morphological taxonomists, *etc.*) to follow.

The special issue begins with an introductory paper by Dr. Barbara Taylor and her colleagues (Taylor *et al.* 2017*b*). This paper details the benefits of developing guidelines and quantitative standards for taxonomy in marine mammals. Taylor *et al.* (2017*b*) note the complicated nature of cetacean taxonomy, elucidating the logistical, historical, and ecological complexities of this group. For example, it is extremely difficult to acquire samples across the widespread geographic range of many cetacean taxa that exist on opposite ends of the globe (*e.g.*, humpback whales, *Megaptera novaeangliae*). Furthermore, unlike terrestrial animals, where mountains, rivers, and other landscape barriers form obvious locations to test for subspecies, there are fewer perceptible physical barriers or ecological breaks in cetacean distributions. While the ocean can have complex thermohaline circulation patterns, isolated gyres, and patchy prey distributions these are often cryptic to human perception, which probably has limited the number of historically proposed subspecies. As molecular genetic data on cetaceans accumulate, identification of cryptic species and subspecies is the norm. But how do we use these molecular genetic data? Here lies the value to this special issue.

This collection of papers helps the reader who may be unfamiliar with molecular genetic analysis all the way from justifying why guidelines and quantitative standards are necessary through a guide to the markers and analytical tools that are being used to make species and subspecies assessments (Rosel *et al.* 2017*b*, Martien *et al.* 2017), and finally to specific guidelines and standards (Taylor *et al.* 2017*a*). In the opening paper Taylor *et al.* (2017*b*) define *subspecies* as “a population, or collection of populations, that *appears to be* a separately evolving lineage with discontinuities resulting from geography, ecological specialization, or other

forces that restrict gene flow to the point that the population or collection of populations is diagnosably distinct.” Martien *et al.* (2017) tackle the issue of using analytical methods with genetic data to identify diagnosably distinct entities. They review seven categories of analytical methods currently used to delimit distinct populations, and find that assignment tests or multivariate methods are particularly good at estimating diagnosability with genetic methods. One of the multivariate methods that shows tremendous promise is Random Forests analysis, which Archer *et al.* (2017) use on DNA sequence data. They show with simulated and empirical data sets that Random Forests produces classification models that are suitable for diagnosing both subspecies and species. This is the first step in identifying a population that is on an independent evolutionary trajectory. New genomic approaches or other sources of data can then be brought to bear on whether a diagnosably distinct population is adapted to a local environment and on a unique evolutionary trajectory.

Other papers in this special issue, tailored for the readers of *Marine Mammal Science*, review the use of molecular genetic markers on marine mammals in the published literature (Rosel *et al.* 2017*b*), and subsequently explore a suite of analytical metrics estimating molecular genetic differentiation across established cetacean populations, subspecies, and species (Rosel *et al.* 2017*a*). Surprisingly, Rosel *et al.* (2017*b*) found that for many genetic studies of cetaceans, sample sizes were good, but the authors found weak geographic sampling for broadly distributed taxa and, more alarming, a lack of articulation of the species or subspecies concept being used to evaluate the data. Rosel *et al.* (2017*b*) clearly demonstrate that improvements could be made to the field by developing guidelines for the molecular genetic study of cetacean taxonomy.

The conclusion reached from these initial five papers is found in Taylor *et al.* (2017*a*). This paper provides a first attempt at establishing an evolving document to provide guidelines that identify the important elements of any molecular genetic study that influences taxonomy. Taylor *et al.* (2017*a*) provides an initial set of quantitative and qualitative guidance on elements like the basis for the taxonomic hypothesis being tested, sample distribution, sample size, number and sequence length of genetic markers, description of approaches to maximize data quality, and analytical methods used to evaluate the genetic data.

While we are sure that some readers may take issue with some of the proposed standards, we hope that articulating these guidelines will lead to lively and productive debate. Such a debate on the use of molecular genetics in taxonomy is currently needed as we are at the beginning of a new molecular genomic revolution, where researchers will have unprecedented power to discern every pod, pack, family group, and cohort. The marine mammal community will be well prepared to advance into the genomics era, having considered many of the issues identified in this special issue.

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