What Exactly is a Species?

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In the Spring 2005 *American Currents*, I offered a primer on zoological nomenclature, using the scientific (or Latin) names of native fishes to teach the importance of nomenclature and why names change over the years (Scharpf, 2005). Yet despite 250 years of naming species, biologists do not agree on what exactly a species is. You'd think a concept so fundamental to the study of biology would be clear and unified, but it's not. Life is so diverse that it resists human efforts to classify it into a convenient and universally agreed-upon fashion. Defining a species is no exception. As a result, a list of native North American fish species compiled by one expert will likely not match a list compiled by another. Nomenclatural changes will account for some differences, but profound scientific and philosophical disagreements on what constitutes a species will likely account for others. Here follows a short review of just a few of the 20-plus species concepts that have been proposed and debated by taxonomists and evolutionary biologists, illustrated with examples from North American freshwater fishes.

How Different Must a Different Species Be?

For many non-biologists, the species concept is a no-brainer: A species is any group of organisms that is morphologically distinct from another. This was the concept employed by Linneaus when he got the practice of identifying and naming species off to its official start in 1753. However, the criteria for determining a sufficient level of morphological difference between closely related species is subjective and arbitrary. There's no rule of thumb for how different a species must be in order to be a different species. A trait that's morphologically distinct to one expert may be interpreted as the natural variation that can occur within a species by another.

A second problem with the Morphological Species Concept (or MSC, to use the official shorthand) is the existence of "sibling" or "cryptic" species (Butler and Mayden, 2003). Cryptic species are usually closely related species that look alike but have different DNA (e.g, the Ozark Madtom, *Noturus albater*, and its chromosomally and biochemically distinct lookalike, the Black River Madtom, *N. maydeni*). In such cases the MSC overlooks discrete forms and underestimates biological diversity.

Species Can't Interbreed, Right?

Clearly, a better definition of a species was needed, and for most of the 20th century biologists thought they had it. First proposed in the 1930s, the Biological Species Concept (BSC) defines a species as a group of interbreeding populations that under natural[1] conditions do not interbreed with other populations. In other words, a species is reproductively isolated from other species. It seems straightforward—a species breeds among itself but can't breed with another species. But nature is rarely straightforward. Some species do interbreed, or hybridize, under natural conditions. For example, White Sucker (*Catostomus commersonii*) and Largescale Sucker (*C. macrocheilus*) hybridize where their distributions overlap in the Columbia River basin but nevertheless maintain separate

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[1] The importance of the adjective "natural" cannot be underestimated. Natural conditions are those caused solely by natural phenomena, i.e., without any influence, involvement or interference from humans. Once an ecosystem has been altered by a human—including the introduction of a species into an area in which it does not naturally occur—the effected organisms are no longer free to follow their own evolutionary fates. Therefore, any interbreeding that occurs when two fish species are forced to live together by humans is considered unnatural and irrelevant to the definition of a species.

genetic identities despite occasionally swapping their genetic material (Nelson, 1968). And as demonstrated among chubs of the American Southwest, hybridization is one way new species can be formed. The Virgin River Roundtail Chub, *Gila seminuda*, to cite one example, is a natural hybrid between *G. robusta* and *G. elegans* (DeMarais et al., 1992).[2]

So if species *can* interbreed . . .

What, Then, is a Species?

Fast forward to the 1960s and the introduction of the Evolutionary Species Concept (ESC). According to the ESC, a species is any independent evolutionary lineage that maintains its identity over space and time from other such lineages and has its own evolutionary tendencies and historical fate.

Let's say a river (undammed, unchanneled and flowing in a pristine, natural state) floods its banks and several individuals of a minnow species are isolated in a nearby fishless spring. The minnows in the spring cannot return to the river, and minnows in the river cannot enter the spring. The spring minnows reproduce and over the years they begin to diverge slightly from the parent population. Let's say their bodies tend to be rounder and chunkier, and their fins tend to be shorter. If you looked at one spring specimen you probably wouldn't be able to distinguish it from a river specimen, but if you looked at 100 spring specimens you notice an overall tendency towards rounder, chunkier bodies and shorter fins. It's clear that the spring form is evolving independently from the river form and maintaining its identity. According to the ESC, this evolutionary independence means the spring minnow constitutes a separate species.

Many evolutionary biologists like the ESC because it's a flexible concept that can accommodate all units of biodiversity, including natural hybrids. Conservation biologists like the ESC too; granting species status to "special" populations can be a powerful tool in protecting the smaller and lesser-known units of biodiversity that are often among the first to disappear. One drawback is that it's a hypothetical concept rather than a hands-on, operational one. How, for example, do you look into the future to confirm that a population will continue to evolve separately (i.e., have its own historical fate)? How do we know that the river will not flood again and wash all the spring minnows back into the river from whence they came? The ESC works great as a conceptual basis for viewing patterns in nature. In fact, the ESC singles out not just the species, but the process of speciation itself. But it's near impossible to actually use the ESC to identify lineages over space and time. For that, biologists still need to rely on more operational concepts like the BSC, and an even newer concept, the PSC.

Developed in the 1980s, the Phylogenetic Species Concept (PSC) defines a species as any group of organisms in which all individuals share a unique derived (apomorphic) characteristic—that is, any characteristic, be it morpholgical, behavioral or genetic—not present in its ancestors or relatives. Put another way, a species is the smallest discernible self-perpetuating cluster of organisms (Kullander, 1999). The degree or size of the difference is not important. Just as long as a group of organisms is distinct in some reliably discernible way, it qualifies as a species. A common objection to the PSC is that it will result in an increase in the number of recognized species. Proponents counter with a big "So what?" If the species are out there, then they should be recognized. What's the advantage of placing an arbitrary limit on the number of species that can be named? Any species concept that conceals biodiversity reduces our ability to inventory, understand, manage, and potentially benefit from this biodiversity.

Which Species Concept is the "Right" One?

They all are, and none of them are, at the same time.

It's important to realize that species may be more of an artificial tool of organization and convenience than it is an actual natural entity. Species don't know that they're species and don't always behave as such; they continue to evolve and find ways to sidestep the rules a "species" is supposed to follow.

To solve the species puzzle, ichthyologist Richard L. Mayden (1999) proposed a hierarchical species concept with the ESC serving as the primary concept and other species concepts serving as secondary ones. The ESC, Mayden argued, has the greatest ability to account for the enormous array of life on this planet, while secondary concepts like the

[2] Hybridization is just one of many criticisms leveled at the Biological Species Concept. Chief among the others is the fact that the criterion of reproductive isolation is impossible to apply to fossil species, and impractical (if not impossible in many instances) to observe in the wild; in both cases researchers have to assume reproductive isolation occurs based on deductions from morphological, ecological, biochemical and ethological (behavioral) evidence. Another flaw of the BSC is that it cannot apply to asexual species. Among North American freshwater fishes, take the example of the Mangrove Rivulus, *Rivulus marmoratus*, of south-eastern coastal Florida. It's the only known self-fertilizing hermaphroditic fish in the world. Each individual has ovaries and testes, and thus is able to fertilize its own eggs. Reproductive isolation cannot be applied to the Mangrove Rivulus or else every individual would qualify as a separate biological species!

BSC and PSC, being more practical or operationally driven, serve as useful tools for discovering and investigating species that are consistent with the primary concept. In some ways, Mayden's idea is consistent with an oft-repeated joke among taxonomists, and which for my dollar stands as the simplest, most honest definition of a species:

A species is what a competent taxonomist says it is!

If the papers currently being published by competent taxonomists are any indication, then it seems that the vast majority of ichthyologists are using the PSC, with many new species being described. Most of these species aren't "new" in the sense that their populations were previously undiscovered. It's just that no one looked at them closely enough to discover just how diverse they really are.

The Orangethroat Darter, *Etheostoma spectabile*, is a case in point. The more ichthyologists look at it, especially at the color differences between breeding males, the more they realize that multiple species (under the PSC) exist. When all is said and done, the "Orangethroat Darter" may actually be 17 (or more) different species (P. Ceas, pers. comm.).

(Note to aquarists: Don't mix your stocks; an Orangethroat Darter from, say, Arkansas, is likely a different species than an Orangethroat Darter from, say, Kansas.)

What About Subspecies?

A final taxonomic sticking point needs to be addressed: subspecies. Struggling with how to catalogue the morphological variation between different populations of the same species, taxonomists have long divided themselves into "splitters" and "lumpers." Splitters like to name well-defined local populations as new species; lumpers prefer to unite local variants into a single species. Biologists began to realize that many clearly identifiable geographic forms were an important intermediate stage between local variants and "good" species. An uneasy compromise was reached: give these "in between" forms a trinomial (third name) and call them subspecies.

Generally, subspecies fall into two categories: local populations that differ genetically from each other and do not interbreed because of a natural barrier, but probably would interbreed if that barrier was removed; and local populations that differ genetically from each other but do interbreed in a hybrid zone where their populations overlap.

Most contemporary taxonomists view subspecies as an artificial construct. If anything, the category of subspecies is indicative of a potential need for further taxonomic study. Quite often these studies (usually following the ESC or PSC) present new data that justify the elevation of subspecies to full species status. But until such studies are completed for all fish groups, and until contemporary species concepts are adopted by all ichthyologists, trinomial names will be retained in some of the field guides and books used by non-scientists.[3]

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[3] Beyond subspecies, federal biologists have their own unit of classification for distinctive groups of Pacific salmon, called an Evolutionary Significant Unit, or ESU. An ESU refers to any salmon population or group of populations that is substantially reproductively isolated from other populations, and represents an important component of the "evolutionary legacy" of the species (Waples, 1991). Most ESUs are characterized by the streams and time of year in which the fish return to spawn (e.g., Upper Columbia River Spring-Run Chinook Salmon). ESUs could, under the strictest application of the ESC, be regarded as full species. And if climatic and geological conditions remained stable for a long enough time, ESUs would presumably evolve into "classic" species under the BSC (Moyle, 2002). Either way, ESUs are treated as is they are full species under the U.S. Endangered Species Act.