

Validating the Taxonomic and Distributional Status of the Neosho Smallmouth Bass (*Micropterus dolomieu velox*)

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Introduction

Classification of the black basses (genus *Micropterus*) has been a circular process (Kassler et al. 2002). The genus was originally described by Bernard Germaine de Lacépède in 1802 (Kassler et al. 2002). His representation of the taxon was generally accepted, but it drew criticism for its insufficient detail and numerous inconsistencies regarding morphological characters (Henshall 1881). Dissatisfaction with the taxonomy encouraged Henshall (1881) and other contemporary naturalists to propose revisions to *Micropterus* that would build upon Lacépède's original descriptions. Taxonomists continued to reconfigure the nomenclature of *Micropterus* over the next few decades. At one point, eight generic and 20 specific names were used to identify unique groups (Ramsey 1975). Names of species changed frequently, and some bass variants were "rediscovered" on several occasions (Long et al. 2015). The genus was eventually consolidated in 1896 by Jordan and Evermann into two broad, distinct taxa known as the Smallmouth (*M. dolomieu*) and Largemouth (*M. salmoides*) Basses. Hubbs and Bailey (1940) later reorganized the black basses as a tribe consisting of two separate genera, namely *Huro*, which housed the Largemouth Bass, and *Micropterus*, which distinguished three species and five subspecies (Hubbs and Bailey 1940). *Huro* was later absorbed into *Micropterus* in a further revision (Bailey and Hubbs 1949). Biologists have worked to refine and understand the taxonomy of *Micropterus* ever since. New species—*M. cataractae*, for example—have been

named as recently as 1999 (Williams and Burgess 1999), and the former subspecies Alabama Bass (*M. henshalli*) was elevated to species status in 2008 (Baker et al. 2008). We currently recognize nine unique species (Shaw 2015).

Historical contention over black bass taxonomy can be partly attributed to their popularity as sport fishes. Their desirability among anglers is nothing new; Henshall (1881), who was well-known for his *Micropterus* enthusiasm, devoted a significant portion of his work to recommending proper tackle and strategy for successful recreational fishing. Many *Micropterus* species are highly sought-after by competitive anglers. Aggressiveness, speed, and relatively large body size are all prized physical traits that make basses entertaining to catch. Because of their relative popularity, smallmouths are important for recreational tourism, and, as such, they can positively impact local economies (Carey et al. 2011). In fact, they are often considered major assets in local communities throughout their native range (Brewer and Long 2015). Sport-fishing has prospered into a billion-dollar industry in the United States (USFWS 2006; Long et al. 2015). As participation in black bass angling has increased, the need for conservation and management policy has become more pressing. Smallmouth Bass (*M. dolomieu*), for example, are highly managed throughout North America (Brewer and Orth 2015). Catch-and-release rules, harvest limitations, and hatchery supplementation for this species are all regulated in a way that maximizes catch rate for anglers and minimizes risk to fish populations (Eland et al. 1996; Lyons et al. 1996; Slipke et al. 1998; Newman and Hoff 2000).

The status of *Micropterus* as a sport fish has contributed to ubiquitous stocking for the purpose of generating fishing opportunities for anglers (Robins and MacCrimmon 1974; Figure 1). Since the mid nineteenth century when it became common (Surber 1935), the practice has

not slowed (Koppelman 2015). Nearly 3 million Smallmouth Bass were released in 1948 (Tunison et al. 1949), and more than 15 million Largemouth Bass were introduced into various reservoirs in 2005 (Siepker and Casto-Yertzy 2008). Stocking often involves the introduction of non-native forms. It is very common with *M. dolomieu*, which has been introduced throughout various regions of the North America within (Stroud and Clepper 1975) and outside its native range (Brewer and Orth 2014). Species like *M. dolomieu* are ideal candidates for stocking because of their general robustness to changing environments (Taylor et al. 2016). However, this adaptability can trigger negative ramifications at the ecosystem level through invasion (Marchetti et al. 2004; Guenther and Spacie 2006), or, perhaps more notably, at the population level through unwanted hybridization.

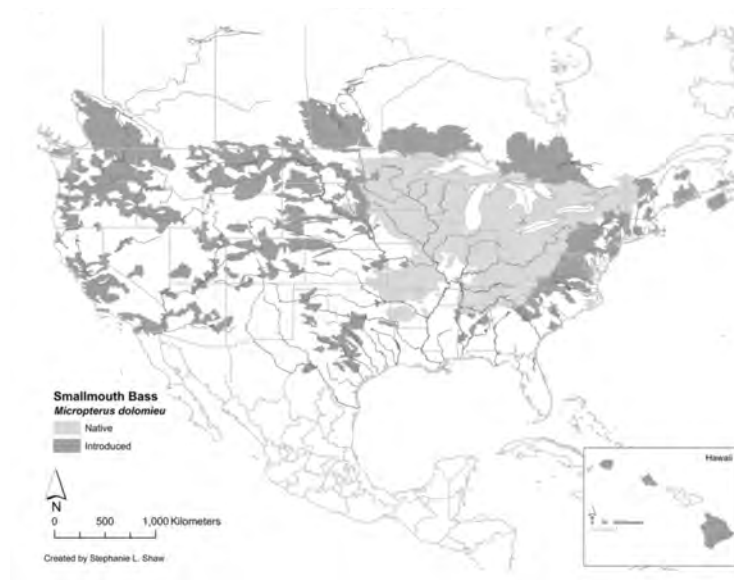


Figure 1. Known distribution of Smallmouth Bass (*Micropterus dolomieu*) in North America. Light grey shaded regions represent the native geographic range of *M. dolomieu*, while dark grey regions indicate areas where both variants of Smallmouth Bass have been introduced (from Brewer and Orth, 2014).

Hybridization—in genetics, the mating of unrelated individuals that differ by at least one gene—is known to occur naturally (Koppelman 2015). A combination of biotic and abiotic mechanisms work to inhibit interspecific reproduction in *Micropterus*, such as courtship, color, or water turbidity, but they are not absolutely isolating (Childers 1975). When populations are subjected to anthropogenic influence through stocking, the process is accelerated (Koppelman 2015). Interbreeding has been documented in cases where allopatric species have been placed together (Morizot et al. 1991). Philipp et al. (1983) demonstrated intermixing between Largemouth Bass and Florida Bass after stocking had taken place. Similarly, Whitmore (1983), Edwards (1979), and Whitmore and Butler (1982) showed hybridization between Guadalupe Bass and introduced *M. dolomieu*. Pierce and Van Den Avyle (1997) also demonstrated hybridization between *M. dolomieu* and Spotted Bass (*M. punctulatus*), noting that hybrid genotypes were seen in as many as 37 percent of individuals from intermixed populations. Their findings were particularly significant given that *M. dolomieu* and *M. punctulatus* are the only sister taxa in *Micropterus* that inhabit overlapping geographic ranges (Near et al. 2003). Hybridization and subsequent genetic introgression between these species has been shown in at least two other studies (Koppelman 1994; Avise et al. 1997). Smallmouth Basses are especially vulnerable to hybridization because of the relative frequency at which they are introduced outside their native range (Lee et al. 1980). Also, since *Micropterus* species are relatively recently-diverged on an evolutionary timescale, and since low divergence can result in higher susceptibility to hybridization, it is important to consider how this process can impact interspecific diversity.

Factors associated with hybridization between non-native congeners, such as introgression of non-native alleles and backcrossing, can decrease the genetic integrity of a population (Barwick et al. 2006; Littrell et al. 2007). These effects can eliminate local adaptations that help to maintain a species' evolutionary capacity (Koppelman 2015; Taylor et al. 2016). In extreme cases, hybridization can lead to total swamping of genetic variation in a subpopulation (Barwick et al. 2006) or potentially outbreeding depression (Wyle et al. 1986; Altukhov and Salmenkova 1987; Stahl 1987; Philipp and Whitt 1991). Non-native black bass genotypes have altogether supplanted native genotypes in some subpopulations (Barwick et al. 2006; Stormer and Maceina 2008; Leitner et al. 2015). Subpopulations with desirable qualities for recreational angling, such as catchability, size and aggressiveness, can be lost when unique genes are threatened (Thrope and Koonce 1981). By diluting a population's genetic makeup, it is possible to reduce overall fitness and increase vulnerability to limiting factors like disease (Hallerman 2003; Goldberg et al. 2005). The risks associated with stocking have fueled controversy in the black bass community over taxonomic assignment (Brewer and Long 2015). To prevent the potential negative impacts of hybridization on genic diversity in bass populations and to avoid ambiguity in classification, it is important to understand the taxonomic and ecological relationships among and within species.

The two subspecies of *M. dolomieu*, The Northern Smallmouth Bass (*M. dolomieu dolomieu*) and the Neosho Smallmouth Bass (*M. dolomieu velox*), provide an informative model for assessing relatively recent genetic divergence. Both groups can be identified by their differential morphology and non-overlapping native ranges. Hubbs and Bailey (1940) describe *M. d velox* as having a combined total of 21 to 23 soft dorsal fin rays and dorsal spines, having a

straight, slender predorsal contour, having a protruding lower mandible, having developed teeth along the tongue, and having dark, broad, less elevated bars in juveniles. In contrast, they characterize *M. d. dolomieu* as having 24 to 25 total soft dorsal rays and dorsal spines, a bulky and more rotund predorsal contour, a non-protruding lower mandible, a lack of teeth along the tongue, and dark, slender, and elevated bars (Hubbs and Bailey 1940). Nearly 80 percent of observed samples could be identified as one or the other based on these meristics (Hubbs and Bailey 1940). Individuals can be distinguished predominately by the slight variation in the number of soft dorsal fin rays, of which *M. d. dolomieu* usually has 14 while *M. d. velox* usually has 13 (Stark and Echelle 1998; Figure 2). Geographically, both subspecies occupy a significant swath of the North American Midwest, with their habitat extending from the southern edge of the Arkansas River Basin to the Saint-Lawrence Great Lakes system near the northern border of the United States (Brewer and Orth 2014). *M. d. dolomieu* is found north and east of the Mississippi River and is not known to inhabit the Interior Highlands. *M. d. velox* is restricted to the lower Ozark Highlands ecoregion (Stark and Echelle 1998; Nigh and Schroeder 2002).

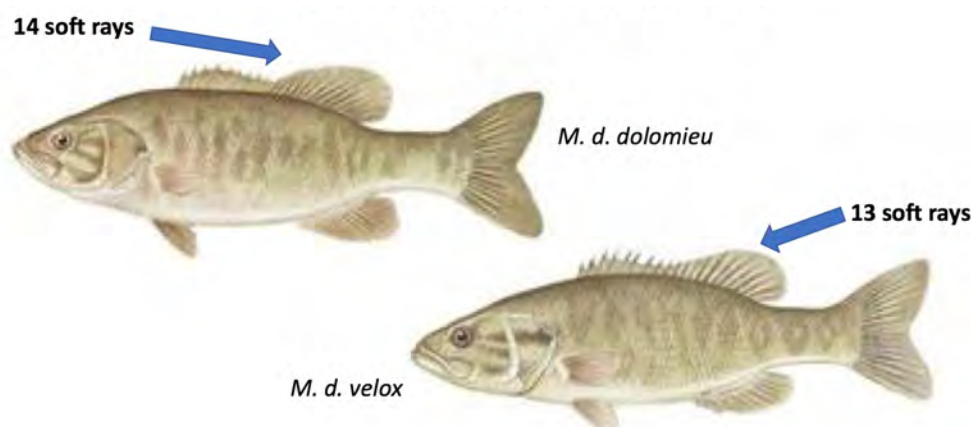


Figure 2. Morphological comparison of Northern Smallmouth Bass (*M. d. dolomieu*; top left) and Neosho Smallmouth Bass (*M. d. velox*; bottom right). Arrows point to groupings of soft dorsal rays, of which *M. d. dolomieu* generally exhibit 14 while *M. d. velox* generally exhibit 13 (Figure from Hubbs and Bailey 1940).

M. d. velox typically occurs in geological landscapes dominated by soluble limestone. Their habitat is defined by a mixture of smooth and rugged, woody plains (Brewer and Long 2015). The combination of their geographic location and geological makeup expose *M. d. velox* to slow-moving streams (Dauwalter and Fisher 2007) that carry limited sediment loads. Although *M. d. velox* has been observed to inhabit turbid, sediment-heavy areas, it is generally found in clear areas (Brewer and Long 2015). Additionally, *M. d. velox* is limited in its distribution by water temperature (Brewer and Long 2015). Only a few studies have tested the tolerance of the Neosho variant to changing temperatures, but it is hypothesized that individuals alter their temperature preferences over the course of their lifetime, moving from warmer to cooler pools (Brewer 2013b). The subspecies is often constrained by these elements of the environment even though its specific habitat preferences can vary depending on life stage and time of year (Todd and Rabeni 1989; Livingstone and Rabeni 1991). *M. d. velox*, like *M. d. dolomieu*, is migratory; individuals travel long distances for overwintering or homing purposes (Webster 1954; Langhurst and Schoenike 1990; Larimore 1952; Fajen 1962). *M. d. velox* mirrors *M. d. dolomieu* in several aspects of its ecology, most notably in habitat choice for spawning (Brewer and Long 2015). However, few studies have compared their ecological adaptation. Regardless, the combination of historical and ecological processes—that is, the processes that have resulted in the geographic isolation among the basses—may have contributed to genetic variation between *M. d. velox* and *M. d. dolomieu* (Borden and Krebs 2009).

M. d. velox and *M. d. dolomieu* have not always been considered unique variants despite their morphological and ecological differences. The early twentieth century taxonomy

was based on pre-genetic tools for comparison, including meristics, scale coloration, and external morphology (Ramsey 1975; Near and Koppelman 2009). Morphological and ecological differences between *Micropterus* species are subtle (Near et al. 2003; Miller 1975; Mabee 1993), making it difficult to determine whether variation is representative of divergent taxa or simply natural variation. Bailey (1956) determined that morphology between the forms was not sufficiently distinct to warrant taxonomic distinction. Hoyt (1973) further suggested that interspecific stocking had altered meristic traits since their original descriptions, ultimately concluding that *M. d. velox* and *M. d. dolomieu* could not be classified as separate subspecies.

Several genetic studies, however, support genetic divergence between *M. d. velox* and *M. d. dolomieu* (Stark 1995; Stark and Echelle 1998). They fit well into Hubbs' notion that many physical traits in aquatic organisms are intimately linked to features of the environment through adaptation (Hubbs and Bailey 1940). Stark and Echelle (1998) found in their analysis of allozymes at 33 gene loci that Smallmouth Basses from the Interior Highlands ecoregion could be classified into three clades, including *M. d. velox*, the Ouachita Smallmouth Bass (currently unnamed), and a separate clade consisting of individuals from multiple streams in the upper Ozark Highlands. This separation was corroborated by principal component analysis based on allele frequencies (Figure 3). Interestingly, most of the diversity within the Smallmouth Basses can be traced to the Interior Highlands in central North America (Malloy 2000). Until the past two decades, the majority of genetic studies have investigated hybridization between *M. d. dolomieu* and non-native congeners in populations east of the Mississippi River (Whitmore and Butler 1982; Whitmore 1983; Whitmore and Hellier 1988; Morizot et al. 1991; Koppelman 1994).

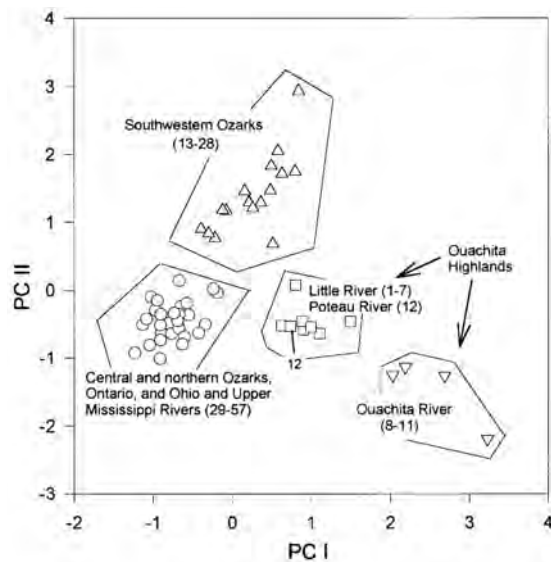


Figure 3. Principal component analysis showing arcsine-transformed allele frequencies among smallmouth bass subpopulations in the Interior Highlands (from Stark and Echelle, 1998).

With the discovery of high diversity in the Interior Highlands, it has become imperative to investigate the effects of stocking on *M. d. velox* in its native tributaries of the Arkansas River Basin. There has been recent interest in stocking Grand Lake o’ the Cherokee’s—a relatively small impoundment in Northwestern Oklahoma—to increase angling opportunities for the surrounding community (Taylor et al. 2016). Taylor et al. 2016 conducted a genetic structure analysis of Interior Highland Smallmouth Bass to determine the degree of introgression of non-native alleles into native *M. d. velox* populations. With this study, they sought to ascertain potential *M. d. velox* broodstock that could be introduced into Grand Lake in place of individuals from a non-native “Tennessee Lake Strain” (Taylor et al. 2016). They identified introgression of non-native alleles in all of their tested populations. Although the level of introgression varied considerably (Taylor et al. 2016; Figure 4). Because of the possibility that intermixing non-native subpopulations can lead to hybridization and loss of co-adapted traits

(Koppelman 2015), Taylor et al. (2016) demonstrated the need for additional investigation into the genetic diversity among Smallmouth Bass.

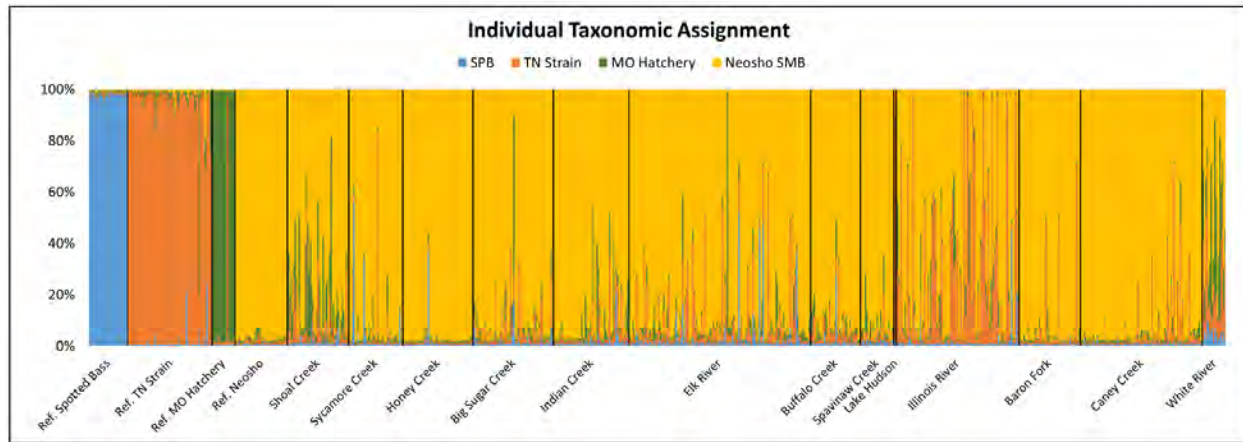


Figure 4: Taxon-level genotype proportions for 873 Smallmouth Bass individuals (represented by individual bars) sampled from the Interior Highlands ecoregion. Assignment estimates were calculated in STRUCTURE using allele frequencies for the four listed taxonomic groups (Spotted Bass (SPB), Tennessee Strain (TN Strain), MO Hatchery, and Neosho SMB)). Within sites (horizontal axis), individual genotypes are organized such that left-to-right corresponds approximately to the upstream-to-downstream direction in the sampled tributary. (Figure and caption adapted from Taylor et al. 2016).

Systems biologists often assume that the designation of novel taxa represents an accurate understanding of evolutionary history (Barracough and Nee, 2001), when, instead, these designations should be examined as testable hypotheses (Bagley et al. 2011). Apposite treatment of taxonomic classification is essential to the conservation and management of biodiversity within and among populations (Nelson and Soule 1987). Stockers and fish biologists have begun to focus their efforts toward black bass conservation in recent years (Tringali et al. 2015). However, without a proper understanding of genetic or morphological variation among species and subspecies, irreparable dilution of genetic diversity within certain subpopulations by introducing non-native forms may be possible or even if table (Nelson and Soule 1987;

Echelle 1991). The genetic identities of Smallmouth Basses are known to be affected by interspecific stocking (Birdsong et al. 2015). To understand the potential impacts of this practice on *M. d. velox*, it is important to evaluate the distinctions of *M. d. velox* and *M. d. dolomieu* as novel subspecies. We cannot rely solely on the historically tenuous morphological distinctions between these subspecies to evaluate their status. Additionally, because of the viability of hybrid offspring in *Micropterus*, the genus does not conform to the Biologic Species Concept. Taxonomic classification should therefore be assessed using the Ecological (Van Valen 1976) and Evolutionary (Simpson 1961) Species Concepts. More specifically, *M. d. dolomieu* and *M. d. velox* must be evaluated against the criteria that they represent separately evolving lineages with their own “unitary roles and tendencies” (Evolutionary Species Concept; Simpson 1961), and that they occupy unique, adaptive zones in which they are “minimally different from that of any other lineage in [their] range” (Ecological Species Concept; Valen 1976).

The gaps in our knowledge of morphological and genetic diversity in *M. d. velox* are disproportionate to the management and conservation efforts that may be required to preserve their diversity (Brewer and Long 2015). For these reasons, it is necessary to validate the taxonomic and distributional status of *M. d. velox*. We propose to investigate the taxonomic and distributional status of *M. d. velox* using molecular tools. More specifically, through microsatellite and genomic analyses, we seek to 1) determine the taxonomic status of the subspecies, and 2) determine the delimited range of the diverged, unique form should it exist.

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