BIODIVERSITY OF MEXICAN TROUT (TELEOSTEI: SALMONIDAE: ONCORHYNCHUS): RECENT FINDINGS, CONSERVATION CONCERNS, AND MANAGEMENT RECOMMENDATIONS

Biodiversidad de Truchas Mexicanas (Teleostei: Salmonidae: *Oncorhynchus*): recientes hallazgos, preocupacion de conservación, y recomendaciones de manejo

RICHARD L. MAYDEN

Department of Biology. 3507 Laclede Ave. Saint Louis University St. Louis, Missouri 63103-2010 USA. maydenrl@slu.edu

ABSTRACT. Until very recently the diversity of trout in Mexican rivers of the Sierra Madre Occidental has been very poorly understood and only the Rainbow Trout, Oncorhynchus mykiss, and the Mexican Golden Trout, O. chrysogaster, have been recognized. Recent efforts in the last decade by a binational organization of scientists and laypersons interested in the diversity and conservation of Mexican trout, Truchas Mexicanus, have revealed considerable diversity within the river systems of the Pacific Slope

south to the Rio Acaponeta. These trout forms are highly differentiated and distinctive, and are considered native to these high-elevation river systems in pine-dominated forests. The increased occurrence of trout growout facilities and hatcheries within the range of these native Oncorhynchus and the escapes from these facilities threaten the native trout diversity through both introgressive hybridization and through resource competition, end products already known to occur in other trout popula-

tions in the other areas of North America exposed to exotic hatchery trout. Other threats to the native and previously unknown trout biodiversity in Mexico include timber harvesting, some pollutions associated with these activities, and siltation of critical habitats. Recommendations are provided to aid in the safe management and protection of this diversity which center around the future use of sterile trout in growout facilities and the use of undisturbed buffer zones along streams. The divergence observed in forms of Mexican trout is equivalent to the levels of divergence found between currently recognized subspecies of trout in the Rainbow and Cutthroat trout groups. Upon review of the diversity and divergence known to exist in these groups and our current understanding of conceptualizations of species, it is argued that the recognition of subspecies within these highly diverse trout lineages is inconsistent with the natural evolutionary history of these groups. The long-term use of the Biological Species Concept for these species is argued as not only inappropriate but an inadequate and illogical characterization of diversity. The logical consequences of hanging on to this concept as the operational and theoretical framework of trout diversity would necessitate the synonymization of all Rainbow and Cutthroat trout taxa as subspecies because of the known propensity of these groups to demonstrate introgressive hybridzation in some areas. These subspecies are considered valid evolutionary lineages that are demonstrate divergence at morphological, genetic, and ecological characters that are well known to many trout taxonomists and biologists. All of these therefore qualify as Evolutionary Species that are easily diagnosable under the Phylogenetic Species Concept and should be recognized as valid species.

Key Words: Biodiversity, Trouts, Conservation, Mexico

RESUMEN. Hasta recientemente la diversidad de las truchas en ríos mexicanos de la Sierra Madre Occidental ha sido entendida pobremente y sólo la trucha arcoiris, Oncorhynchus mykiss, y la trucha dorada mexicana, O. chrysogaster, han sido reconocidas. Los esfuerzos recientes durante la última década por una organización binacional de científicos y legos interesados en la diversidad y conservación de las truchas mexicanas, han revelado una considerable diversidad dentro de los sistemas fluviales de la vertiente Pacífica al sur del Río Acaponeta. Estas formas de truchas están altamente diferenciadas y distintas, y son consideradas nativas a estos sisemas riverinos de alta elevación en bosques dominados por pino. La creciente presencia de establecimientos para la crías de truchas y piscifactorías dentro del área de estas Oncorhynchus nativas y los escapes de estas facilidades amenazan la diversidad de truchas nativas a consecuencia de ambas, hibridización introgresiva y por competencia por recursos, y productos finales ya conocidos por suceder en otras poblaciones de truchas en otras areas de Norte América expuestas a truchas exóticas de criadero. Otras amenazas a las truchas y diversidad nativas previamente desconocidas in México incluyen tala de bosques, alguna polución asociada a esta actividades, y el azolve de hábitats criticos. Se proveen recomendaciones para ayudar en el manejo seguro y la protección de esta diversidad que se centran sobre el uso futuro de truchas esteriles en las instalaciones de engorda y el uso de zonas buffer no perturbadas a lo largo de las corrientes. La divergencia observada en las formas de trucha Mexicana es equivalente a los niveles de divergencia que se encuentran entre las subespecies actualmente reconocidas

de subespecies de trucha en los grupos arcoiris y cuello cortado. Sobre la revisión de la diversidad y divergencia que se sabe existe en estos grupos y nuestro entendimiento actual de las conceptualizaciones de especies, se argumenta que el rconocimiento de subespecies en estos linajes altamente diversos es inconsistente con la historia natural evolutiva de estos grupos. El prolongado uso del Concepto de la Especie Biológica para estas especies se argumenta que no sólo es inapropiado sino tambien una inadecuada e ilógica caracterización de la diversidad. Las consecuencias lógicas de apegarse a este concepto como el armazón operativo y teórico de la diversidad de truchas necesitaría la sinonimización de todos los taxa de trucha arcoiris y cuello cortado como subespecies debido a la propensión conocida de estos grupos de mostrar hibridización introgresiva en algunas áreas. Por lo contrario, estas "subespecies" son consideradas linajes evolutivos válidos que demuestran divergencia en caracteres morfológicos, genéticos, y ecológicos que son bien conocidos a muchos taxónomos y biólogos de truchas. Todas ellas en consecuencia califican como Especies Evolutivas que son fácilmente diagnosticables bajo el Concepto de Especies Filogenéticas y deben ser reconocidas como especies válidas.

Palabras Clave: Biodiversidad, Truchas, Conservación, Mexico

INTRODUCTION

Most scientists and laypersons alike are very familiar with the North American trout species of the genus Oncorhynchus from their popularity in angling, aquaculture, and as a food resource. Likewise, most of these same

people know of North American trout diversity almost entirely because of the common Rainbow Trout, Oncorhynchus mykiss (formerly known as Oncorhynchus or Salmo gairdneri), a species that is the dominate "form" used in stocking streams from hatcheries or "grow out facilities" to appease the avid fishermen. The Rainbow Trout is also known as a distinct lineage with a number of distinctive forms currently referred to as subspecies (Table 1), all inhabiting streams of western North America. Unfortunately, this trout is also famous as a species that has been introduced into just about every possible stream outside of its native range where conditions are tolerable. Other North American trout that are likely of interest to many include the cutthroat trout complex (O. clarki), which also consists of a large number of subspecies under this single polytypic species (Table 1), and the California Golden Trout (O. mykiss aguabonita), the latter species gaining its notoriety for its beautiful colors and demand in fishing. Some of the less commonly known species in North America include the Gila Trout (O. gilae gilae), Apache Trout (O. g. apachae), and the various forms of rainbow and cutthroat trout concealed as subspecies under presumed single lineages. The recent publications by Behnke (1992, 2002) discussing trout diversity and hypotheses as to their origins and the heroic efforts by national organizations focusing on the restoration and conservation of trout and their habitats have brought considerable attention to the existence and diversity of these aguatic predators, especially in the United States. In fact, today, unlike a few decades ago within the United States there is considerable emphasis on the management of native trout and "bringing back the natives" rather than a need for introducing "hatchery" rainbows for fishing pleasure. Trout advocates have been exceedingly successful

in drawing attention to the protection of some trout and salmon species, subspecies, and ESUs (Evolutionarily Significant Units; Nielsen, 1995), restoration of habitats for native taxa, elimination of exotic trout populations, and management of wild populations within the United States borders.

Few, however, are probably familiar with the diversity of trout species and subspecies of the rivers draining the western face or Pacific Slope of the Sierra Madre Occidental in Mexico. Most probably know only of the Mexican Golden Trout (O. chrysogaster), introduced or native populations of the "Rainbow Trout" O. mykiss, and the Baja California Rainbow Trout (O. mykiss nelsoni). In fact, except for the exceptionally beautiful Mexican Golden Trout most probably think of trout diversity south of the border as simply "more Rainbow Trout." In fact, until just recently we really knew very little as to the diversity of native trout or truchas nativas in the rivers of Mexico, except for O. mykiss nelsoni (see Hendrickson et al., 2002 for recent review). Interestingly, scientists have known about the occurrence of native Mexican trouts for over a century but they have received very little study except for a few investigations between 1930 and 1960's (Hendrickson et al., 2002). With the exception of these few studies and the occasional comparison or mention of Mexican trout, other than the Mexican Golden Trout, very little is known of the mainland trout diversity and biology of the Sierra Madre Occidental, despite the fact that they range from the Río Yaqui in Sonora and Chihuahua south to the Río Acaponeta, Durango (Hendrickson et al., 2002; Ruiz-Campos et al., 2003). Within the last decade a binational cooperative research group, Truchas Mexicanus, has focused their efforts on revealing the natural distribution and diversity of trout in Mexico, educate both the people and Mexican and United States government of this diversity, determine possible threats to the diversity, and identify reasonable conservation and management efforts that can be developed to carry on this exceptional natural resource of biological diversity of Mexico (Fig. 1). Hendrickson et al. (2002) provides a detailed review of not only the history of trout in Mexico but also some aspects of our current understanding of these fishes. Herein, I review some of the efforts of *Truchas Mexicanus* towards studying these species, including the diversity of native species known from Mexican riverine ecosystems, the context of this diversity with respect to other trout from North America, the current environmental and anthropogenic threats to this diversity, and offer recommendations on conservation and management for consideration.

RESULTS AND DISSCUSION

Diversity and Distribution

The native range of trout from mainland Mexico includes northwestern Pacific Slope arroyos and rivers, and most probably similar headwaters of the Río Conchos Drainage (Rio Grande Basin), draining the high-elevations of the Sierra Madre Occidental. The exact distribution of native populations has been somewhat debated by biologists since the 1960's. However, given the recent, more extensive sampling efforts through Truchas Mexicanus, it is believed that this is largely because of the very few collections and field studies that have been made on these fishes prior to 1995 and the limited knowledge that biologists writing on native trout of Mexico have had on the diversity and relationships of these organisms. Given that most sampling of trout in Mexico has occurred at most easily accessible locations, usually bridges on highways, and most of the native trout occur in remote, high-elevation ecosystems knowledge of this diversity prior to the efforts of *Truchas Mexicanus* must be considered with caution. Recent efforts by biologists working as part of *Truchas Mexicanus* have demonstrated that native and diverse forms of trout exist in mainland rivers from the Río Yaqui, southward to the ríos Baluarte and Acaponeta (Needham and Gard, 1959; Lindsey, 1960; Miller, 1960; Miller and Smith, 1986; Minckley et al., 1986; Hendrickson et al., 2002). Some controversy existed as to the origin of trout populations south of the Río Culiacán and those occurring in endorheic basins of the Casas Grandes or Guzmán system on the east side of the continental divide in Chihuahua (Behnke, 1992; Needham and Gard, 1959) and the upper Río Conchos.

Until very recently, largely as a result of a concern for the conservation of native trout from Mexico, these fishes have never been comprehensively studied for morphological and genetic diversity, distribution, and ecology (Hendrickson et al., 2002). Recent field studies indicate that native trout exist in Mexico from the Río Yaqui southward to the Río Acaponeta, and possibly slightly further south. Based on the recent field, morphological, and genetic investigations those populations south of the Río Culiacán are native; it is likely, however, that populations from the Río Casas Grandes had their origin in the Río Yaqui and were transported by humans. The status of trout in the upper Río Conchos remains unresolved. While literature descriptions indicate that trout were found in this drainage, recent sampling has not yet revealed any populations. However, it should be recognized that the geographic areas inhabited by these fishes is very remote and very difficult to reach and sample thoroughly, warranting caution as to any concrete statements as to the lack of trout from some rivine systems of the Sierras.

While Behnke (1992) has argued that the trout diversity of Mexico consists of basically two taxa, Mexican Golden Trout (O. chrysogaster) and Rainbow Trout (O. mykiss), it has becoming increasingly clear that such a view of diversity is incomplete. Morphological studies by Ruiz-Campos et al. (2003) and unpublished data by participants of Truchas Mexicanus, using both morphological and genetic diversity, unequivocally demonstrate that multiple, unique evolutionary lineages of trout are native to Mexico, in addition to O. chrysogaster, and these undescribed taxa are not O. mykiss. Furthermore, the origins and relationships of these trout have been poorly known, but with the possible exception of the Río Conchos diversity, are likely part of a major clade of distinct forms within a larger "Rainbow Trout lineage" inclusive of multiple distinct forms warranting recognition as species. It is likely that the trout of the upper Río Conchos is part of a Cutthroat Trout lineage even though no species of this lineage is currently known from Mexico (Hendrickson et al., 2002). Current estimates of diversity include possibly two distinct forms of the Mexican Golden Trout and multiple undescribed trout endemic to different rivers or river groups both north and south of the latter species complex. These species are diagnosable on the basis of morphological traits and molecular markers identified by Ruiz-Campos et al. (2003) and being studied by biologists of Truchas Mexicanus. Both Hendrickson et al. (2002) and Ruiz-Campos et al. (2003) provide excellent illustrations by Joseph R. Tomelleri and photographs of these distinct forms, respectively. Descriptions of this diversity will be forthcoming.

Threats to Native Mexican Trout Diversity

The most daunting and permanent threats to the native

trout diversity of Mexico includes both abiotic and biotic pollution. Abiotic factors include land and water usage and the main biotic factors include the importation of the exotic hatchery bred "Rainbow Trout," considered the same species by some, into the streams via hatcheries and "growout" facilities for trout. Trout and relatives of in Salmonidae are cold-water adapted species and require a constant source of clear, clean, and cold waters for their survival. The restriction of native populations to high-elevation rivers in pine-dominated forests is a clear indication of their niche demands as these rivers provide the only habitats in their native range where they can maintain a phylogenetically constrained physiology and feed effectively visually. Lower elevation habitats in the same river systems may appear to have appropriate habitats for native trout but the water is both too turbid for sight feeding and too warm for the high metabolic demands of their physiology.

This requisite habitat type is being lost in North America through land use practices that include logging of areas by gross clear-cutting and harvesting trees down to the banks of the river or arroyos. Harvesting of lumber for commercial use harbors one of the most devastating impacts for these fishes because of the rate and magnitude that this occurs in these ecosystems. The logging activities eliminate natural shade for these aquatic habitats and result in increased water temperatures that are intolerable to trout. Furthermore, these practices create marginal habitat for trout but offer preferred habitats for competitive native and non-native, non-trout species. The activities associated with clear cutting (total elimination of all plant life and disruption and compaction of soils) lead to the loss of topsoils and errosional activities increasing the turbidity of streams and loss of microhabitats for both trout and their food resources. Runoff flowing into streams rap-

idly increases turbidity and its slow deposition into the once clean substrate prevents the percolation of water through the gravel and cobble, leading to depletion of oxygen levels for invertebrates naturally inhabiting these areas. Eventually, stream banks become heavily eroded, the clear and cool flowing water habitat is lost, and the substrate becomes impacted by sediments. These logging activities will also lead to the introduction of undesirable contaminates emanating from sawmills, including sawdust spoils, into streams that significantly alter water chemistry to the detriment of different aquatic organisms, including trout. Maintaining this type of critical habitat for the permanent existence of trout will require attention to protecting these systems from the introduction of pollutants and at least forested buffer zones along streams to both shade appropriate habitats and serve as silt sieves to prevent erosional degredation of habitats.

Of an equally devastating order to the native trout populations of Mexico is the existence of the exotic or introduced hatchery Rainbow Trout, O. mykiss. The introductions of non-native fishes can lead to native fishes being eliminated by competition for resources, including food and spawning habitats, extreme predation pressures, and introgressive hybridization swamping of native genomes and gene pools of trout, all leading to the extirpation or extinction of native fish diversity. Previous studies of trout within the United States have unequivocally demonstrated that the introduction of hatchery bred Rainbow Trout into ecosystems will likely lead to these fishes elminating native taxa (subspecies or species) either through resource competing or hybridization (Behnke, 1992, 2002; Campton and Utter, 1985; Carmichael et al., 1993; Carmichael et al., 1996; Dowling and Childs, 1992; Hitt et al., 2003; Leopold, 1918; Moyle et al., 1986; Propst

et al., 1992; Weigel et al., 2003). History in the US has clearly demonstrated that the introduction of hatchery trout or the transportation of trout to non-native waters is an illadvised practice and will lead to extinction. The Yellowfin Cutthroat Trout, O. c. macdonaldi, is a perfect example of irresponsible introductions of "conspecific" trout into the same lake environment that ultimately lead to the extinction of this taxon. While these mistakes are now realized by most State and Federal fisheries personnel, considerable damage and some extinction has resulted from these activities. Hatchery Rainbow Trout, "O. mykiss," have been widely introduced into many streams across the United States, Canada, and many other countries world wide, largely for fishing purposes; in nearly every instance, this has lead to the loss of native fish diversity in areas where trout are not native because of intense predatory pressures of a new predator. These hatchery predators have been introducted into many spring habitats throughout the United States and rivers and lakes in other countries where they have completely depleted the native fish faunas, amphibian species, and many macroinvertebrates endemic to the systems, all in the name of recreational fisheries

In Mexico small hatcheries or "growout" facilities housing non-native Rainbow Trout speckle the landscape in the Sierras. Each of these facilities requires cool fresh water and will be located on arroyos or headwater streams where water can be diverted into the system for trout production. These facilities provide not only income for those maintaining them but also a food resource for locals and are considered mostly desirable by local communities. If managed properly, these facilities can be of a limited threat to native trout populations existing in the same waterways; however, this is difficult to maintain. Hatchery Rainbow

Trout are known to routinely escape even the best-constructed facilities and the inevitable washouts occurring with regular high-water levels lead to the introductions of non-natives into stream systems, mixing with native species.

Other pressures on native trout diversity like pollution (other than sawmills) and recreational fishing pressures, because of the current remote locations of most populations, do not appear to be a major threat. However, with the general growth of human populations in some areas in Chihuahua, Sonora, and Durango, especially in areas with headwater streams, these will eventually be factors impacting native fish and other aquatic organisms.

Conservation and Management Recommendations

The maintenance of natural diversity of trout in Mexico requires a public appreciation for this natural and cultural heritage, and secondarily, the promotion of "wise use" activities associated with the logging and fisheries industries of the areas inhabited by the species and in Mexico, in general. Timber harvesting and hatchery development will naturally occur within the range of native trout because of resource needs and the realized profits associated with these resources. It is impossible and illogical to expect that these activities will be discontinued, especially when they continue to flourish in other nations, including the United States in the face of environmental degradation. However, there are measures that should be considered as important action items to minimize the impact of detrimental activities on native species.

The two most important items that could, in large part, preclude the loss of native trout diversity include the stocking of sterile trout into hatcheries and growout facilities and the maintenance of naturally forested and undisturbed

buffer zones along streams. These two efforts will not only significantly improve the likelihood of continued existence of native trout species but will also help to insure the long-term existence of quality water supplies in these areas, the continued supply of trout as a food source, and the likely growth of fishing and ecotourism in the areas harboring native species, thereby offering alternative sources of income for local communities. Other important action items that must be considered include public education in communities as to the negative impacts of non-native trout being introduced into streams as a result of poorly constructed holding facilities and human-facilitated releases, the negative impacts of translocation of native species, the impacts of sawmill and other pollutants on stream ecosystems, and the broad impact of pollutants in aquatic systems.

Maintenance of native stock strains for hatchery purposes for the different sub-basins of Mexico does not seem feasible as this will be cost prohibitive, and has a high likelihood of generating additional problems through genetics of breeding systems and an increased chances of accidental introductions of different stocks into different stream systems. However, public appreciation of the diverse forms of trout in small sub-basins, the promotion of these as a food source for local rearing activities, and public education as to the negative impacts for their own ecosystems of the alternatives, will likely significantly improve the long-term maintenance of this trout diversity. Long-term maintenance, protection, and/or public appreciation of natural habitats for trout species is especially critical; most loss of biodiversity occurs through the loss of their natural habitats and the occurrence of the exotic Rainbow Trout in these streams can be classified as a type of biotic pollution to these ecosystems.

Unfortunately, the American people and State and Federal agencies of the United States were ignorant of the great biodiversity of native trout species, in part because of the long-standing negligence and incomplete understanding of the evolutionary history of these fishes and appropriate taxonomy. The continued recognition by many biologists and agencies of the great diversity of North American trout as a composite of subspecies, despite important and adequate evidence of divergence at morphological and molecular characteristics disputing the polytypic nature of the "Rainbow Trout" and "Cutthroat Trout" lineages, is an insult to the natural heritage of the New World and has had devastating outcomes for these fishes. Many mistakes have occurred through translocations of these so-called "subspecies" into another "subspecies" range and the "purity" of these taxa has been compromised, some "subspecies" have gone extinct because of introductions of "conspecifics," and many of the natural habitats have been damaged through both biotic and abiotic pollution because these fishes were all considered "Rainbow Trout." The situation has begun to change in the last decade as more people have become increasingly more conscious of the logical inconsistencies of the taxonomy and the impact that poor management practices have had on these species. However, this has only occurred after permanent damage to the natural diversity has occurred. In Mexico the present-day situation of hatchery influence and logging is not very widespread because of the remote locations of many of the rivers, and the opportunities exist to prevent a "biodiversity train wreck" for Mexican trout if responsible actions are instituted immediately. Therefore, as basic recommendations to the local, State, and Federal agencies responsible for maintenance and protection of natural biological diversity in Mexico and aquaculture practices the following items are offered as recommendations:

- 1. Recognize and promote in local communities and schools the diversity of native trout in Mexico and other aquatic life forms
- 2. Provide general education through brochures, videos and documentaries as to the importance of healthy aquatic ecosystems for both the aquatic species and for humans
- 3. Develop educational materials regarding the various types of biotic and abiotic pollutants that will negatively impact aquatic ecosystems
- 4. Provide educational information to local communities and schools as to the negative impacts of exotic trout released into streams
- 5. If stocking occurs only use sterile trout in hatcheries and growout facilities
- Maintain undisturbed forested buffer zones along streams
- 7. Provide educational information to local communities as to the important effects buffered stream banks versus the clear cutting of forests without maintenance of riparian habitat.

These actions should also be augmented through cooperative interactions between biologists and agencies in Mexico, United States and Canada on native trout species biologies and protection. Through *Truchas Mexicanus* and support from the National Science Foundation we have already initiated early educational efforts with hatchery personnel in Mexico visiting hatchery facilities all associated with either U. S. Fish and Wildlife Service, Arizona Game and Fish, and Mexico Game and Fish and all maintaining native trout species. These efforts should be continued and enhanced through bi- or tri-national meet-

ings of biologists, conservation organizations, NGOs, and regulatory agencies to aggressively address the emerging demise of the diversity of native trout species in Mexico. Having already been through the loss of trout species diversity and habitat north of Mexico, personnel from these agencies can readily provide critical advise on the maintenance of this grand diversity, especially if funding from private and national and international organizations and agencies can be acquired to support these efforts.

Perspectives on North American Trout Diversity

As currently promulgated by Behnke (1992, 2002) there are only four species of trout in the Rainbow Trout and Cutthroat Trout lineages (Table 1), plus other species of Oncorhynchus and species in the genera Salmo and Salvalinus. This long-standing perception of the species diversity in Oncorhynchus is extremely conservative, especially given the morphological and genetic divergence that is exhibited across these taxa and the diversity of ecological fidelity found in some instances. Relative to the evolutionary divergence in most other groups of fishes found in the New World the currently recognized trout diversity referred to as subspecies would unequivocally be considered distinct species and would be attributed the same full protection and public recognition as distinct evolutionary entities, and not simply geographic variants within the Rainbow Trout or Cutthroat Trout lineages. The reality of the situation with North American trout diversity is that for decades most trout taxonomists and geneticists have held and yielded the Biological Species Concept but have recognized diversity on its "propensity" to interbreed with other such diversity in a particular purported lineage. However, the classification that has dominated is one that derives from an inconsistent application of the meaning

of the "ability to interbreed" under the Biological Species Concept and an inconsistent application of morphological and genetic divergence. In no instance has the ability to interbreed been experimentally tested and applied where appropriate for the subspecies of Rainbow Trout or Cutthroat Trout. Rather, these taxa are recognized as subspecies because of an opinion that they have not reached a stage of reproductive isolation, presumably a conclusion reached because of levels of some type of operational criterion of divergence. However, levels of divergence is neither a logical nor defensible argument for the current recognition of these taxa as subspecies because many of the subspecies are as divergent or more divergent for molecular, chromosomal, ecological, and morphological traits as these "Rainbow Trout" or Cutthroat Trout" are to the Gila, Apache, or Mexican Golden Trout. The ability to interbreed as a criterion for subspecies is illogical given that Rainbow Trout and Cutthroat Trout lineages interbreed in some instances and in some locations to the extent of notbable introgressive hybridization (Campton and Utter, 1985; Dowling and Childs, 1992; Hitt et al., 2003; Moyle et al., 1986); the same occurs for Gila and Apache trout. and and have been inconsistent in their arguments for recognitions of diversity. Finally, there are no substantive thorough analyses of phylogenetic relationships of these taxa to defend the real existence of Cutthroat and Rainbow trout lineages as currently conceived. While it seems likely that these groupings may be real, there are not comprehensive studies including all of the diversity demonstrating the monophyly of these groups. If group membership is based on general phenetic similarity of Rainbow-like or Cutthroat-like phenotypes then one may have to reconsider this given that sampling efforts in distant regions of Mexico and rivers of Russia, both currently argued to have only O. mykiss, there are morphotypes that appear phonetically similar to some O. clarki forms.

Many different perceptions of biological species have been developed for recognizing natural products of descent (Mayden, 1997, 1999, 2002). Some of these concepts are clearly better guiding principles or operational tools useful for revealing products of descent with modification (Mayden, 1997, 1999, 2002). The Biological Species Concept employed by many trout biologists, including Behnke (2002), is neither operational for these trout species nor a good guiding principle for recognizing species of fishes in general. In no case has the Biological Species Concept been employed experimentally by bioloaists or taxonomists to demonstrate that the diversity of trout in North America is at the "subspecies level," validly recognized as only 4 independent lineages. Rather, if one were to employ either the Taxonomic, Morphologial, or Genetic species concepts (Mayden and Wood, 1995; Mayden 1997) all of the currently recognized subspecies would be clearly validated as distinct species; all of these taxa are differentiated from one another and are diagnosable, making them demonstrably natual species under the Phylogenetic Species Concept. Likewise, the ability to diagnose taxa or identify monophyletic groupings is evidence for species recognition using any of the versions of the Phylogenetic Species Concept (Mayden and Wood, 1995). Understandably, with the long, unchallenged tradition of the Biological Species Concept during the early active years of discovery of trout taxa and the perpetuation of this concept in academic arenas during the 1950's to the 1970's it is expected that these taxa would have been seen as subspecies under a polytypic species concept like the Biological Species Concept. However, the

science of systematics and taxonomy has matured tremendously in the last 30 years, as has associated disciplines in the philosophy of science and nature, the development of morphological and molecular tools, and how the biological and evolutionary communities are interpreting biological variation and diversity. Many groups of organisms once thought to consist of a "polytypic species" have been seriously reevaluated and reconsidered; the evidence, from a variety of character types, has corroborated these groups as complexes of species, some cryptic, that are now considered distinct and used in scientific fields as important models for natural diversity. The current state of recognizing polytypic species of trout is inconsistent with the recognized patterns of morphological and molecular diversity in these groups; these purported subspecies should be recognized as valid species. In addition to the evidence that is known to exist and reviewed by Behnke (2002) on morphological and molecular divergence of these taxa, it is not even clear that all of the "subspecies" of Rainbow Trout or Cutthroat Trout form monophyletic groups where all of the respective subspecies are closest relatives.

It is therefore argued that the various subspecies currently recognized under Oncorhynchus clarki and O. mykiss represent valid species and should receive full recognition in the scientific and public communities as such. The character evolution data currently available for trout in North America support these subspecies as distinct evolutionary lineages or species sensu the Evolutionary Species Concept (Wiley and Mayden 2000a, b, c; Mayden, 1997, 1999) and diagnosable species sensu the Phylogenetic Species Concept (Mayden and Wood, 1995; Mayden, 1997, 1999), and recognizing either the Rainbow Trout or the Cutthroat Trout as single species is a poor reflection of existing evolutionary diversity within these com-

plexes. Through more detailed investigations of many of these species it is inevitable that additional diversity will be discovered, many of which will likely need protection, and should be described to account for the natural evolutionary products of descent within this fascinating group of fishes. I thank to Dr. Salvador Contreras-Balderas for translate the Abstract.

LITERATURE CITED

BEHNKE, R.J. 1992. Native trout of western North America. American Fisheries Society, Bethesda, Maryland. 275 pp. BEHNKE, R.J. 1992. Trout and Salmon of North America. The

Free Press, New York, New York.

- CAMPTON, D. E., AND F. M. UTTER. 1985. Natural hybridization between steelhead trout (Salmo gairdneri) and coastal cutthroat trout (Salmo clarki clarki) in two Puget Sound streams. Can. J. Fish Aquat. Sci. 42:110-199.
- CARMICHAEL, G.J., J. N. HANSON, M. E. SCHMIDT AND D. C. MORIZOT. (1993) Introgression among apache, cutthroat, and rainbow trout in Arizona. Trans. Am. Fish. Soc. 122:121-130.
- CARMICHAEL, G. J., J. N. HANSON, J. R. NOVY, K. J., MEYER, AND D. C. MORIZOT. 1996 Apache trout management: Cultured fish, genetics, habitat improvements, and regulations. *In Schramm*, H.J. and Piper, R.G., (eds.) Uses and Effects of Cultured Fishes in Aquatic Ecosystems. American Fisheries Society, Bethesda, Maryland.
- DOWLING, T. E., AND M. R. CHILDS. 1992. Impact of hybridization on a threatened trout of the southwestern United States. Conservation Biology 6:355-364.
- HENDRICKSON, D. A., H. ESPINOSA PÉREZ, L. T. FINDLEY, W. FORBES, J. R. TOMELLERI, R. L. MAYDEN, J. L. NIELSEN, B. JENSEN, G. RUIZ CAMPOS, A. VARELA ROMERO, A. VAN DER HEIDEN, F. CAMARENA AND F. J. GARCIA DE LEÓN, 2002. Mexican native trouts: a review of their history and current systematic and conservation status.). Rev. Fish Biology and Fisheries, Vol. 12: 273 316.

- HITT, N. P., C. A. FRISSELL, C. C. MUHLFELD, AND F. W. ALLENDORF. 2003. Spread of hybridization between native westslope cutthroat trout, Oncorhynchus clarki lewisi, and nonnative rainbow trout, Oncorhynchus mykiss. Can. J. Fish. Aquat. Sci. 60:1440-1451.
- LEOPOLD, A. 1918. Mixing trout in western waters. Trans. Am. Fish. Soc. 47:101-102.
- LINDSEY, C. C. 1960. (Review of) Rainbow trout in Mexico and California with notes on the cutthroat series, by P.R. Needham and R. Gard. Copeia 1960:160-162.
- MAYDEN, R. L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem, p. 381-424. *In*: Species: The Units of Biodiversity. Claridge, M.F., Dawah, H.A. and Wilson, M.R. (eds). Chapman and Hall Ltd., London.
- MAYDEN, R. L. 1999. Consilience and a hierarchy of species concepts: Advances towards closure on the species puzzle. Journal of Nematology 31:95-116
- MAYDEN, R. L. 2002. On biological species, species concepts and individuation in the natural world. Fish and Fisheries 2002:171-196
- MAYDEN, R. L., AND R. M. WOOD. 1995. Systematics, species concepts, and the evolutionary significant unit in biodiversity and conservation biology, p. 58-113. *In: J. L. Nielson (ed.).* Evolution and the aquatic environment: defining unique units in population conservation. Am. Fish. Soc. Symposium 17, Bethesda, Maryland.
- MILLER, R. R. 1960. (Review of) Rainbow trout in Mexico and California with notes on the cutthroat series, by P.R. Needham and R. Gard. Progressive Fish-Culturist 22:94.
- MILLER, R.R.AND M. L. SMITH. 1986. Origin and geography of the fishes of central Mexico. *In* Hocutt, C.H. and Wiley, E.O., (eds.) The Zoogeography of North American Freshwater Fishes. John Wiley & Sons, Inc., New York, pp. 487-517.
- MINCKLEY, W.L., D. A. HENDRICKSON AND C. E. BOND. 1986. Geography of western North American freshwater fishes: description and relations to intracontinental tectonism. *In* Hocutt, C.H. and Wiley, E.O. (eds.) Zoogeography of Western North American Freshwater

- Fishes. John Wiley and Sons, New York, NY, pp. 519-613. MOYLE, P. B., H. W. LI, AND B. A. BARTON. 1986. The Frankenstein effect: impact of introduced fishes on native fishes in North America, pp. 415-426. *In*: R. H. Stroud
- (Ed.) Fish culture in fisheries management. American Fisheries Society, Bethesda, Maryland.
 NEEDHAM, P.R., AND R. GARD. 1959. Rainbow trout in Mexico

and California with notes on the cutthroat series. Universi-

- ty of California Publications in Zoology 67:1-124.

 NEEDHAM, P.R., AND R. GARD. 1964. A new trout from central Mexico: Salmo chrysogaster, the Mexican golden trout.

 Copeia 1964:169-173.
- NIELSEN, J. 1995. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society. Symposium 17. Bethesda, Maryland
- PROPST, D.L., J. A. STEFFERUD AND P. R. TURNER. (1992) Conservation and status of Gila trout, Oncorhynchus gilae. Southwest. Nat. 37:117-125.
- RUIZ-CAMPOS, G., F. CAMARENA-ROSALES, A. VARELA-RO-MERO, SERGIO SANCHEZ-GONZALEZ, JORGE DE LA ROSA-VELEZ. 2003. Morphometric variation of wild trout populations from northwestern Mexico (Pisces: Salmonidae). Rev. Fish Biology and Fisheries, Vol. 13: 91 - 110
- WEIGEL, D. E., J. T. PETERSON, AND P. SPRUELL. 2003. Introgressive hybridization between native cutthroat and introduced rainbow trout. Ecol. Appl. 13:271-289.
- WILEY, E. O., AND R. L. MAYDEN. 2000a. The evolutionary species concept, p. 70-89. *In*: Species Concepts and Phylogenetic Theory: A Debate (Q. D. Wheeler and R. Meier, eds.) Columbia University Press, New York, New York.
- WILEY, E. O., AND R. L. MAYDEN. 2000b. Comments on Alternative species concepts, p. 146-158. In: Species Concepts and Phylogenetic Theory: A Debate (Q. D. Wheeler and R. Meier, eds.) Columbia University Press, New York, New York.
- WILEY, E. O., AND R. L. MAYDEN. 2000c. A reply to our critics, p. 198-208. *In*: Species Concepts and Phylogenetic Theory: A Debate (Q. D. Wheeler and R. Meier, eds.) Columbia University Press, New York, New York.



Fig. 1. Official logo of *Truchas Mexicanus*, a binational organization of scientists and laypersons committed to better understanding diversity, conserving, and protecting native trout species in the rivers of Mexico.

Taxonomy by Behnke (2002)		Taxonomy Recommended Herein	
Scientific Name	Common Name	Scientific Name	Common Name
Oncorhynchus chrysogaster	Mexican Golden Trout	Oncorhynchus chrysogaster	Mexican Golden Trout
Oncorhynchus gilae			
O. g. gilae	Gila Trout	O. gilae	Gila Trout
O. g. apachae	Apache Trout	O. apachae	Apache Trout
Oncorhynchus mykiss (Rainb	ow Trout, eight subspecies)		
O. m. irideus	Coastal Rainbow Trout	O. irideus	Coastal Rainbow Trout
O. m. gairdneri	Columbia River Rainbow-Redband Trout	O. gairdneri	Columbia River Rainbow Trou
O. m. whitei	Little Kern River Golden Trout	O. whitei	Little Kern River Golden Trou
O. m. gilberti	Kern River Rainbow Trout	O. gilberti	Kern River Rainbow Trout
O. m. aguabonia	South Fork Kern River Golden Trout	O. aguabonia	South Fork Kern River Golden
Trout			
O. m. stonei	Redband Trout	O. stonei	Redband Trout
O. m. newberrii	Redband-Rainbow Trout	O. newberrii	Redband-Rainbow Trout
O. m. nelsoni	Baja California Rainbow Trout	O. nelsoni	Baja California Rainbow Trou
O. m. ssp.	Mexican Rainbow Trout Subspecies	O. sp.	Yaqui Trout
		O. sp.	Mayo Trout
		O. sp.	Presidio Trout
		O. sp.	Baluarte Trout
		O. sp.	Acaponeta Trout
Oncorhynchus clarki (Cutthro	oat Trout, fourteen subspecies)		
O. c. clarki	Coastal Cutthroat Trout	O. clarki	Coastal Cutthroat Trout
O. c. lewisi	Westslope Cutthroat Trout	O. lewisi	Westslope Cutthroat Trout
O. c. bouvieri	Yellowstone Cutthroat Trout	O. bouvieri	Yellowstone Cutthroat Trout
O. c. behnkei	Snake River Finespotted Cutthroat Trout	O. behnkei	Snake River Cutthroat Trout