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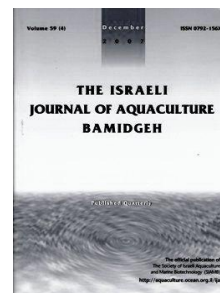
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Conservation genetics of tilapias: Seeking to define appropriate units for management

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Key words: Conservation, evolutionary significant unit, management unit, tilapia

Abstract

Tilapias comprise 112 species and subspecies of cichlid fishes of the genera *Oreochromis*, *Sarotherodon*, and *Tilapia*. Because of the importance of tilapias to aquatic ecosystem structure and function, fisheries, and aquaculture, it is critically important to conserve wild genetic resources. Of the 112 recognized tilapia taxa, 41 are regarded as imperiled. In order to manage adaptively important genetic variation in tilapias, we need to recognize and define biologically appropriate units of conservation. An evolutionary significant unit (ESU) can be defined as a population or group of populations that merits priority for conservation and separate management because of high genetic and ecological distinctiveness from other such units. Management units (MUs) are defined as populations that are demographically independent of one another; that is, their population dynamics depend mostly on local birth and death rates, and not on genetically effective migration. Identification of MUs – similar to “stocks” widely referred to in fisheries management – is useful for short-term management, such as managing habitat, delineating fishing areas, setting harvest rates, and monitoring population status. Against this background, the goal of our review and synthesis was to summarize knowledge and recommend critical work yet to be done regarding conservation of tilapias, approaching this task in a species-by-species manner. With the exceptions of *Oreochromis niloticus*, *O. mossambicus*, and *Sarotherodon melanotheron*, the body of existing work regarding genetic and adaptive differentiation of populations of tilapias is insufficient to inform identification of evolutionary significant units, a knowledge gap that should be addressed by targeted research. We note that competition and interspecific hybridization caused by introductions of tilapias for aquaculture purposes jeopardizes the genetic resources of certain native tilapia species. We hope that our review and synthesis spark critical discussion of tilapia conservation within the tilapia aquaculture, management, and conservation communities.

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3 Conservation genetics of tilapias: Seeking to define appropriate units for management

Introduction

Need for conservation of tilapias. The tilapias comprise 112 species and subspecies of cichlid fishes of the genera *Oreochromis*, *Sarotherodon*, and *Tilapia* (FishBase, 2013, Table 1).

Table 1. Valid species and subspecies of tilapias (Fishbase 2013), with conservation status as assessed by the International Union for the Conservation of Nature (IUCN 2013). IUCN's levels of imperilment from least to greatest are: LC (LC), Near Threatened (NT), V (V), Endangered (E), Critically Endangered (CE), Extinct in the Wild (Ex.W), and Extinct (Ex). The table also includes Not endangered (NE)

Latin Name	Conservation Status	Threat(s)
<i>Oreochromis amphimelas</i>	E	Growth overfishing, effects of drought on shallow lakes
<i>Oreochromis andersonii</i>	V	Competition with introduced <i>O. niloticus</i> , overfishing with no refuge areas
<i>Oreochromis angolensis</i>	LC	
<i>Oreochromis aureus</i>	NE	
<i>Oreochromis chungruruensis</i>	CE	Restricted to small crater lake subject to fluctuation in water level, siltation
<i>Oreochromis esculentus</i>	CE	Competition with introduced <i>O. niloticus</i> , predation by introduced Nile perch, overfishing, siltation, pollution, changes in plant community
<i>Oreochromis hunteri</i>	CE	Siltation, seasonal drought, weed-infestation
<i>Oreochromis ismailiaensis</i>		Data deficient
<i>Oreochromis jipe</i>		
<i>Oreochromis karomo</i>	CE	Overfishing, habitat alteration due to agriculture
<i>Oreochromis karongae</i>	E	Overfishing, population collapsed in 1990s
<i>Oreochromis korogwe</i>	LC	
<i>Oreochromis lepidurus</i>	E	Pollution from transportation, oil disposal; future threats from dam and aluminum mining
<i>Oreochromis leucostictus</i>	LC	
<i>Oreochromis lidole</i>	E	Overfishing, population collapsed in 1990s
<i>Oreochromis macrochir</i>	V	Competition with introduced <i>O. niloticus</i> in certain systems
<i>Oreochromis mortimeri</i>	CE	Competition with introduced <i>O. niloticus</i>
<i>Oreochromis mossambicus</i>	NT	Competition and hybridization with introduced <i>O. niloticus</i> .
<i>Oreochromis mweruensis</i>	LC	
<i>Oreochromis niloticus baringoensis</i>	NE	
<i>Oreochromis niloticus cancellatus</i>	NE	
<i>Oreochromis niloticus eduardianus</i>	NE	
<i>Oreochromis niloticus filoa</i>	NE	
<i>Oreochromis niloticus niloticus</i>	NE	
<i>Oreochromis niloticus sugutae</i>	NE	
<i>Oreochromis niloticus tana</i>	NE	
<i>Oreochromis niloticus vulcani</i>	NE	
<i>Oreochromis pangani girigan</i>		Poss. synonymous w/ <i>O. jipe</i>
<i>Oreochromis pangani pangani</i>		Poss. synonymous w/ <i>O. jipe</i>
<i>Oreochromis placidus placidus</i>	LC	Fished; threat of hybridization with <i>O. niloticus</i>
<i>Oreochromis placidus ruvumae</i>	LC	
<i>Oreochromis rukwaensis</i>	V	Overfishing, siltation, pollution
<i>Oreochromis saka</i>	NE	
<i>Oreochromis salinicola</i>	V	Mining, use of toxic plants for fishing, overfishing
<i>Oreochromis schwebischi</i>	LC	
<i>Oreochromis shiranus chilwae</i>	NE	
<i>Oreochromis shiranus shiranus</i>	NE	
<i>Oreochromis spilurus niger</i>	NE	
<i>Oreochromis spilurus percivali</i>	NE	
<i>Oreochromis spilurus spilurus</i>	NE	
<i>Oreochromis squamipinnis</i>	E	Overfishing, population collapsed in 1990s

(Table I cont.) Latin Name	Conservation Status	Threat(s)
<i>Oreochromis tanganycae</i>	LC	
<i>Oreochromis upembae</i>	LC	
<i>Oreochromis urolepis hornorum</i>	NE	
<i>Oreochromis urolepis urolepis</i>	NE	
<i>Oreochromis variabilis</i>	CE	Overfishing, competition with introduced <i>O. niloticus</i> , predation by introduced Nile perch
<i>Sarotherodon caroli</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution, water withdrawal
<i>Sarotherodon caudomarginatus</i>	LC	
<i>Sarotherodon galilaeus borkuanus</i>	NE	
<i>Sarotherodon galilaeus boulengeri</i>	NE	
<i>Sarotherodon galilaeus galilaeus</i>	NE	
<i>Sarotherodon galilaeus multifasciatus</i>	NE	
<i>Sarotherodon galilaeus sanagaensis</i>	NE	
<i>Sarotherodon knauerae</i>	NE	
<i>Sarotherodon lamprechtii</i>	NE	
<i>Sarotherodon linnellii</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution, water withdrawal
<i>Sarotherodon lohbergeri</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution, water withdrawal
<i>Sarotherodon melanotheron heudelotii</i>	NE	
<i>Sarotherodon melanotheron leonensis</i>	NE	
<i>Sarotherodon melanotheron melanotheron</i>	NE	
<i>Sarotherodon mvogoi</i>	LC	
<i>Sarotherodon nigripinnis dolloi</i>	NE	
<i>Sarotherodon nigripinnis nigripinnis</i>	NE	
<i>Sarotherodon occidentalis</i>	NT	Drought, deforestation, overfishing, dams
<i>Sarotherodon steinbachi</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution, water withdrawal
<i>Sarotherodon tournieri liberiensis</i>	NE	
<i>Sarotherodon tournieri tournieri</i>	NE	
<i>Tilapia bakossiorum</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution
<i>Tilapia baloni</i>	LC	
<i>Tilapia bemini</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution
<i>Tilapia bilineata</i>	LC	
<i>Tilapia brevipinnis</i>	LC	
<i>Tilapia busumana</i>	V	Deforestation; sedimentation; pollution from agriculture, mining, and sewage; invasive aquatic plants
<i>Tilapia buttikoferi</i>	LC	
<i>Tilapia bythobates</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution
<i>Tilapia cabrae</i>	LC	
<i>Tilapia cameronensis</i>	LC	
<i>Tilapia camerunensis</i>	V	Agriculture-induced sedimentation and pollution

5 Conservation genetics of tilapias: Seeking to define appropriate units for management

(Table I cont.) Latin Name	Conservation Status	Threat(s)
<i>Tilapia cessiana</i>	CE	Deforestation and siltation
<i>Tilapia coffea</i>	CE	Deforestation and mining-induced siltation and pollution
<i>Tilapia congica</i>	LC	
<i>Tilapia dageti</i>	LC	
<i>Tilapia deckerti</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution
<i>Tilapia discolor</i>	V	Agriculture, urban development, mining, deforestation
<i>Tilapia ejagham</i>	NE	
<i>Tilapia flava</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution
<i>Tilapia fusiforme</i>	NE	
<i>Tilapia guinasana</i>	CE	Groundwater withdrawal, potential competition with and predation by <i>O. niloticus</i> , potential hybridization with <i>T. sparrmanii</i>
<i>Tilapia guineensis</i>	LC	
<i>Tilapia gutturosa</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution
<i>Tilapia imbriferina</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution
<i>Tilapia ismailiaensis</i>		Data deficient
<i>Tilapia jallae</i>	NE	
<i>Tilapia joka</i>	V	Agricultural, urbanization, deforestation
<i>Tilapia konkourensis</i>	NE	
<i>Tilapia kottae</i>	E	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution
<i>Tilapia louka</i>	LC	
<i>Tilapia margaritacea</i>	LC	
<i>Tilapia mariae</i>	LC	
<i>Tilapia nigrans</i>	NE	
<i>Tilapia nyongana</i>	LC	
<i>Tilapia pra</i>	NE	
<i>Tilapia rendalli</i>	LC	
<i>Tilapia rheophila</i>		Data deficient
<i>Tilapia ruweti</i>	LC	
<i>Tilapia snyderae</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution
<i>Tilapia sparrmanii</i>	LC	
<i>Tilapia spongotroktis</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution
<i>Tilapia tholloni</i>	LC	
<i>Tilapia thysi</i>	CE	Natural catastrophe (i.e., crater lake 'burping' of CO ₂), deforestation and agriculture-induced sedimentation and pollution
<i>Tilapia walteri</i>	NT	Narrow range; no known threats
<i>Tilapia zillii</i>	NE	

Tilapias are mostly freshwater fishes, and inhabit shallow streams, rivers, ponds, and lakes; certain species have considerable ability to tolerate salinity, commonly live in brackish water, and can disperse through seawater (Chervinski, 1982; Philppart and Ruwet, 1982; Villegas, 1990; review by Cnaani and Hulata, 2011). Tilapias often comprise a vital component of aquatic ecosystems in which they live (Lowe-McConnell, 1982, 2000), playing roles as filter feeders, herbivores, foragers, and detritivores (Maitipe and De Silva, 2006), in turn serving as prey for other species.

Tilapias are of major importance to artisanal fisheries in Africa (Bayoumi and Khalil, 1988; Kolder, 1993) and the Levant (Gophen et al., 1983). Their widespread introduction has led to establishment of tilapia fisheries in areas in which they were not native (Chandrasoma, 1986; Blanco et al., 2007) or not historically an important component of the catch (Balirwa, 1992). Global fisheries harvest of tilapias is approximately 700,000 tons for all species collectively, of which Nile tilapia comprises 287,000 tons (FAO, 2012).

Tilapias are critically important to world aquaculture, as attested to by many contributions to this and previous symposia (Fishelson and Yaron, 1983; Pullin et al., 1988, 1996; Costa-Pierce and Rakocy, 1997; Fitzsimmons, 1997), as well as edited compilations (Lim and Webster, 2006). There have been numerous studies of the performance of aquaculture stocks (Eknath et al., 1993; Hulata et al., 1993; Dey et al., 2000; Rutten et al., 2004; Eknath and Hulata, 2009). Molecular genetic differentiation of aquaculture stocks is relatively well characterized (McAndrew and Majumdar, 1983; Macaranas et al., 1995; Romano-Eguia et al., 2004). The genome of Nile tilapia has been mapped (Lee et al., 2005), and segregation of loci affecting expression of certain aquaculturally-important traits has been detected (Cnaani et al., 2003, 2004; Moen et al., 2004; Shirak et al., 2006; Eshel et al., 2012; Lühmann et al., 2012).

Because of the importance of tilapias to aquatic ecosystem structure and function, fisheries, and aquaculture, it is critically important to conserve wild genetic resources (Pullin et al., 1997, 1999; Lind et al., 2012). After checking the 112 tilapia species and subspecies listed in FishBase (2013) against the International Union for the Conservation of Nature's Red List of Endangered Species (IUCN, 2013), we noted that 41 were regarded as being in some degree of imperilment (Table 1), with 24 of these 41 regarded as Critically Endangered. Yet, this species-level view understates conservation concern. First, some newly described species (e.g., *S. knaueri*, *S. lamprechtii*, *T. ejagham*, *T. fusiforme*, and *T. nigrans*, species endemic only to Lake Ejagham, Cameroon) have narrow distributions and likely are vulnerable to extinction, but have not yet been evaluated for conservation status. Second and more pertinent to our review and synthesis, considering tilapia conservation at the species level while neglecting divergence among evolutionary lineages within species understates the degree of conservation concern. Some well-distributed tilapia species (*O. niloticus*, *O. spiluris*, and *S. galilaeus*) were not evaluated by IUCN presumably because they are secure at the species level, although individual subspecies may be in some degree of imperilment. Further, evolutionarily significant variation below the subspecies level remains largely unaddressed. This concern is not unique to tilapias. Against this background, it becomes clear that while previous assessments have addressed issues of genetic conservation of tilapia species, none have yet related the status of knowledge on particular species to key current concepts in conservation genetics. In this review and synthesis, we aim to advance discussion of conservation genetics of tilapias. We start by briefly describing key concepts in conservation genetic theory, and then turn to an assessment of our understanding of natural adaptive and molecular genetic differentiation of tilapias.

Defining the units of conservation. The goal of conservation genetics is to conserve adaptively important genetic variation. The process begins with recognition and definition of the biologically appropriate units of conservation. However, species protection legislation and the early conservation literature focused on species and subspecies. Mayr and Ashlock (1991, p. 43) define a subspecies as an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of that species. They note, however, that every local population is slightly different from every other local population, as can be established by sufficiently sensitive phenotypic measurements, molecular markers, and statistics. Most critically, they note that no non-arbitrary criterion defines the category of "subspecies", nor is the subspecies a unit of evolution except where it happens to coincide with a geographic or genetic isolate (Mayr and Ashlock, 1991, p. 43). Since conservation aims to protect the adaptive potential of a focal group in a changing ecological context, focusing on the unit of evolution is critical. The relevance of subspecies to conservation has been much debated and mostly rejected (Bruford, 2009).

The key modern concept for defining the unit for conservation is the evolutionary significant unit (ESU), which can be defined as a population or group of populations that merits priority for conservation and separate management because of high genetic and ecological distinctiveness from

7 Conservation genetics of tilapias: Seeking to define appropriate units for management

other such units (Allendorf and Luikart, 2007). Different principles underlie different definitions of ESU, leading to somewhat different criteria for defining ESUs. Ryder (1986) was the first to use the term, defining ESUs as populations that represent significant adaptive variation based on concordance between sets of data derived from different techniques. The concept of an ESU came into wide discussion during deliberations regarding protection of salmonid stocks under the U.S. Endangered Species Act. Waples (1991) proposed that a population warrants protection as an evolutionarily significant unit if it satisfies two conditions: (1) it must be reproductively isolated from other conspecific units, although it does not have to be absolutely isolated, and (2) it must be an important component of the evolutionary legacy of the species. To be considered an important component of the evolutionary legacy, a population must satisfy at least one of the following criteria: (1) the population is genetically distinct, (2) the population occupies unique habitat, (3) the population exhibits unique adaptation to its environment, or (4) if it went extinct, it would be a significant loss to the ecological or genetic diversity of the species. ESUs have been regarded as populations that are distinctive based on morphology, geographic distribution, population demographic parameters, and genetic variation (Dizon et al., 1992). Taking a phylogenetic viewpoint, Moritz (1994) defined ESUs as populations that are reciprocally monophyletic for mitochondrial DNA variation and show significant divergence of allele frequencies at nuclear loci, an approach that defines practical criteria for recognizing ESUs but does not consider adaptive variation. Focusing on adaptive variation, Crandall et al. (2000) regarded ESUs as populations that lack: (1) "ecological exchangeability", i.e., that have different adaptations or selection pressures (resulting in different life histories, morphologies, quantitative trait variation, habitat, or predators) and different ecological roles within a community, and (2) "genetic exchangeability", e.g., no recent gene flow, and show concordance between phylogenetic and geographic discontinuities. The concept and implementation of the ESU framework have been the subject of much discussion within the conservation and fisheries management communities (Nielsen, 1995).

Differences in underlying principles and ESU criteria have led to controversy in practical conservation in some cases. Nonetheless, substantial overlap in criteria regarding reproductive isolation, adaptive differentiation and concordance across multiple data types is such that there is consensus that application of the ESU concept can support rational decision making regarding conservation of populations or groups of populations, whether or not actions are being considered within the context of imperiled species protection.

Perhaps the best-developed applications of the ESU concept within the aquatic sector pertain to Pacific salmonids, and we select such a case study to illustrate its application. In 1994, the U.S. National Marine Fisheries Service (NMFS) initiated a Pacific coast-wide status review of sockeye salmon (*Oncorhynchus nerka*). The biological review team examined genetic, life history, biogeographic, geologic, and environmental information in the process of identifying ESUs. In particular, genetic data; physical, chemical, and biological characteristics of nursery lakes; sockeye salmon river entry and spawn timing; and smolt outmigration timing were found to be most informative for this process. Based on this examination, the team identified six sockeye salmon ESUs and one provisional ESU (Gustafson et al., 1997). Illustrative descriptions of two such ESUs are as follow. The Okanogan River ESU within the Columbia River drainage of Washington is differentiated from other such groupings because of: 1) use of a very eutrophic lake-rearing environment, Lake Osoyoos, which is unusual for sockeye salmon, 2) the tendency for a relatively large percentage of the Okanogan River sockeye salmon population to return as 3-year-olds, 3) juvenile outmigration-timing differences between Okanogan River and Lake Wenatchee-origin fish, 4) adaptation of Okanogan River sockeye salmon to much higher temperatures during adult migration in the Okanogan River, and 5) allozyme data indicating that this population is genetically distinct from other sockeye salmon in the Columbia River drainage. The Quinault Lake ESU includes all sockeye salmon that spawn in the Quinault River drainage and develop as juveniles in Quinault Lake. Early river-entry timing, protracted adult run timing, extended lake residence prior to spawning, unusually lengthy spawn timing, unusual skin pigmentation of spawners, and genetic differences from other coastal Washington sockeye salmon are important factors characterizing this ESU.

Management units (MUs) are defined as populations that are demographically independent of one another (Allendorf and Luikart, 2007), meaning that their population dynamics depend mostly on local birth and death rates, and not on genetically effective migration from other spawning

assemblages. Identification of MUs – similar to “stocks” widely referred to in fisheries management – is useful for short-term management, such as managing habitat, delineating fishing areas, setting harvest rates, and monitoring population status. An ESU may contain multiple MUs; for example, fish populations often are structured at hierarchical levels, such as rivers (which each may contain an MU) that are nested within a watershed (which collectively may contain an ESU). MUs generally do not show long-term independent evolution or strong adaptive variation. Critically, MUs represent populations that are important for the long-term persistence of the ESU to which they belong. Offering an operational definition, Moritz (1994) suggested that MUs are populations that have substantially divergent allele frequencies at many loci. One possible limitation of this approach, however, is that allele frequency differentiation cannot be interpreted directly as evidence for demographic independence (Allendorf and Luikart, 2007). A related issue is the difficulties to determine whether migration from nearby spawning assemblages would be sufficient to reestablish an MU should it become overharvested or extinct. Palsboll et al. (2007) proposed that the identification of MUs from population genetic data be based upon the amount of genetic divergence at which populations become demographically independent; MU status would be assigned when the observed estimate of genetic divergence is significantly greater than a pre-defined threshold value. To illustrate the application of the MU concept, we turn to another case study involving sockeye salmon. Fisheries managers manage local populations separately so that an adequate number of individuals from each local population escapes catch and reproduces to ensure the persistence of the local populations (i.e., the MUs) that make up a fished salmon stock. Ramstad et al. (2004) analyzed approximately 100 sockeye salmon from 11 spawning sites throughout the Lake Clark drainage of the Bristol Bay system in Alaska at 11 microsatellite DNA loci in order to determine whether these spawning assemblages are demographically isolated. The effective population size, N_e , for each of the Lake Clark spawning sites is ~ 1000 or slightly greater. Using the criterion of at least 10% exchange (Hastings, 1993), groups spawning at these sites would be demographically isolated if they exchanged fewer than about 100 adults, which corresponds to genetic differentiation (F_{ST}) of 0.0025 under a classical Wright–Fisher island model of migration-drift equilibrium. Therefore, we would conclude that these spawning sites constitute separate MUs if their genetic divergence, F_{ST} , exceeds 0.0025. The overall value of F_{ST} among these sites excluding one outlier was ~ 0.007 (95% CI of 0.004–0.010). This being greater than the threshold of 0.0025, the authors concluded that these 11 spawning aggregations were demographically isolated and should be considered separate MUs.

Once the units for conservation, the ESUs and MUs, have been identified, conservation planning turns toward addressing the threats to these units. Threats to tilapia species include habitat degradation, overfishing, competition with introduced species (including invasive tilapias), hybridization with introduced tilapias, and predation by introduced species, as discussed below. Against this background of theory and case studies in application of conservation genetics, the goal of our review and synthesis study was to summarize knowledge and recommend critical work yet to be done regarding genetic aspects of conservation of tilapias. We approached this task in a species-by-species manner, considering case studies of selected tilapia species, and conclude by offering some general observations. We consider tilapias narrowly, leaving to other authors important issues about conservation of the non-tilapiine cichlids that constitute species flocks in the African Rift lakes and elsewhere (Meyer et al., 1990; Lowe-McConnell, 1991; Goldschmidt, 1996; Barlow, 2000; Kocher, 2004; Egger et al., 2007).

Species-by-species consideration of conservation genetics

For each case study, we offer a brief description of the species’ range, its economic importance, and its conservation status. We review knowledge of its conservation genetics and assess its adequacy for designation of ESUs and MUs. We close each section by suggesting what studies might be done to fill key data gaps. We start with the simple and move to the complex, first discussing straightforward cases involving narrow endemic species, and then moving to more complex cases for polytypic species.

Species endemic to one waterbody or watershed. Narrow endemics pose straightforward conservation assessments. The simplest case is where a species occurs in just one waterbody or watershed. Several such cases are known in tilapias. *Oreochromis chunguruensis* occurs only in

9 Conservation genetics of tilapias: Seeking to define appropriate units for management

Lake Chunguru, a crater lake in the Rungwe Mountains, north of Lake Malawi in Tanzania. *O. hunteri* is endemic to Lake Chala, Kenya. *O. rukwaensis* occurs only in Lake Rukwa in Tanzania. *O. salinicola* is known only from saline springs near the Lufira River in the Democratic Republic of Congo. *Sarotherodon caroli* is endemic to Lake Barombi Mbo, Cameroon. *T. coffea* occurs only in the St. Paul River, Liberia. In these simple cases where a species occurs in only one waterbody, so long as there is one demographic unit within that waterbody, the MU and the ESU are one and the same. We note several cases where multiple endemic species occur in one waterbody or watershed. *S. knaueri*, *S. lamprechtii*, *T. deckerti*, *T. ejagham*, and *T. fusiforme* occur only in Lake Ejagham, Cameroon. *T. flava*, *T. guttarosa*, *T. imbriferina*, *T. snyderae*, *T. spongotroktis*, and *T. thysis* are endemic to Lake Bermin, Cameroon. *O. saka* and many haplochromine cichlids occur only in Lake Malawi. Such cases suggest the occurrence of sympatric speciation, suggesting the need for molecular study of systematics, including mtDNA-based phylogenetic studies, and for study of behavioral and feeding studies to gain understanding of any sympatric speciation processes, as have been conducted for Lake Victoria and Lake Malawi cichlids (Goldschmidt, 1996; Barlow, 2000). More pertinent to the interests of this review and synthesis, such species and ecosystems should be regarded as high priority for conservation, with planning focused on minimizing threats to the species, its habitat, and ecosystem health.

Species with geographically restricted distributions. A number of tilapia species have distributions that, while restricted, are broader than one waterbody or watershed. For example, *O. amphimelas* has a restricted distribution in sodic waters of the African rift lakes (Lakes Manyara, Eyasi, Kitangiri and Singida in Tanzania), where drought and fishing with small-meshed nets have decimated populations, leading to a decline in the number of mature individuals and periodic loss of habitat (Bayona, 2006). Severe drought often has killed large numbers of fish in these shallow (5–6 m deep) lakes. As the population is restricted to five lakes, the species was assessed by IUCN as Endangered. Parts of Lakes Manyara and Tarangire fall within a National Park where exploitation is prohibited. Populations in each lake, which are demographically independent, would be regarded as MUs. Populations from the protected park areas of Lake Manyara and Tarangire River form an important seed stock for the replenishment of the heavily fished populations in the two areas, exemplifying management of MUs. To our knowledge, no assessment of population genetics or adaptive variation has been performed to assess ESUs within the species.

Species with geographically broad distributions, but no subspecific taxa.

Oreochromis mossambicus. – Mossambique tilapia, *O. mossambicus*, is distributed in standing waters, and inhabits reservoirs, rivers, creeks, drains, swamps and tidal creeks (FishBase 2013). It is commonly found over mud bottoms, often in well-vegetated areas, as well as warm weedy pools of sluggish streams, canals, and ponds. It is common in blind estuaries and coastal lakes, but usually absent from permanently open estuaries and open sea. It can grow and reproduce in fresh, brackish and seawater. Its native distribution includes the lower Zambezi, Lower Shiré, and coastal plains from the Zambezi delta to Algoa Bay. It occurs southwards to the Brak River in the Eastern Cape Province and in the Transvaal in the Limpopo system of South Africa. *O. mossambicus* has been introduced for aquaculture, and has escaped and established itself in the wild in many countries, often outcompeting local species and causing adverse ecological impacts. *O. mossambicus* is an important fisheries resource in Mozambique and has had an important role in socioeconomic development as a source of animal protein, improvement of the human diet, employment generation, and promotion of regional development for poverty alleviation. Both aquaculture and inland fisheries of *O. mossambicus* contribute significantly to supporting food security. Yet, lack of knowledge of the genetic resources of *O. mossambicus* constrains their sustainable and effective use for expansion of fisheries and aquaculture in Mozambique (NEPAD, 2005).

Three studies have considered molecular genetic differentiation of wild *O. mossambicus* populations. Agustin et al. (1997) examined variation at 42 allozyme loci and mitochondrial control region DNA sequences in three wild populations of *O. mossambicus* from the Limpopo and Incomati River systems of South Africa. Differentiation among wild populations was quantified at $F_{ST} = 0.02$ for allozymes and 6.3% sequence divergence for mitochondrial DNA (mtDNA); however, the limited geographic scope of sampling limits the utility of these findings for purposes of delineating conservation units for the species. D'Amato et al. (2007) sequenced 385 bp of the mtDNA control

region and characterized variation at five microsatellite loci in wild and farmed *O. mossambicus*, wild and farmed *O. niloticus*, and morphologically apparent hybrids collected from the wild. One of their aims was the delineation of ESUs for *O. mossambicus*. Among their key findings, within a median joining network of mtDNA haplotypes, the *O. mossambicus* group was composed of three clusters. Cluster *a* occurs mainly at southern locations and cluster *c* at the northernmost sampling sites; both lineages co-exist in the Olifants River and Kasinthula, Malawi. The northern lineage was regarded as ancestral, the southern as representing a recent Holocene radiation. A maximum parsimony tree placed a single haplotype inhabiting the Zambezi basin into a *b* cluster basal to the other two clusters. The authors appropriately cautioned that the differentiation among wild *O. mossambicus* samples should be revisited after sampling more populations lying between the apparent northern and southern population groupings; hence, the data presented should be regarded as preliminary for delineating ESUs, although a set of working hypotheses and recommendations can be drawn. They also noted that several population units of conservation value might be recognized within lineages; the populations of the Boesmans River and Usuthu/Pongola may be considered representative of two ESUs within the southern lineage, but their geographic extent must be verified. The authors recommended that their study be extended to geographically close rivers of different basins and to assess the levels of gene flow.

Affecting management of conservation units was interspecific hybridization of *O. mossambicus*, an issue to which we return below. Simbine et al. (2014) used microsatellite loci to evaluate local populations of *O. mossambicus* from the Limpopo, Incomati, Umbeluzi and Sabié Rivers of southern basins of Mozambique. Low but significant values of Φ_{st} (0.006, $P < 0.001$) and D_{est} (0.032, $P < 0.05$) showed that some level of population disconnectivity may occur. These low levels of population differentiation may be explained by floods during the year 2000 (Schneider, 2003; MICOA, 2007) that may have connected local populations of the southernmost Mozambique drainages.

The genetic integrity of many *O. mossambicus* populations is threatened by hybridization with the rapid spread of *O. niloticus* by anglers and aquaculturists (Cambray and Swartz, 2007). Hybridization already is occurring throughout the northern part of the species' range, with most of the evidence coming from the Limpopo River system of South Africa (Weyl, 2008). The threat posed by *O. niloticus* is widespread, although more than half of the locations likely are not yet affected. Given the rapid spread of *O. niloticus*, IUCN anticipates that *O. mossambicus* will qualify as threatened due to rapid population decline through hybridization. The species therefore is assessed as Near Threatened. IUCN recommends that river systems not yet invaded by Nile tilapia must be protected from deliberate and accidental introductions of that species. *O. mossambicus* has been widely introduced for aquaculture, and has escaped and established itself in the wild in many countries, often outcompeting local species (Kottelat and Whitten 1996). Several countries have reported adverse ecological impacts after introduction (FishBase 2013).

Oreochromis esculentus. – The Singida tilapia *O. esculentus* was originally endemic to Lake Victoria, and is now more broadly distributed, including Lake Victoria, Lake Nabugabo, Lakes Kyoga and Kwana, and the Victoria Nile above Murchison Falls, the Malawa River and Lake Gangu, west of Lake Victoria. The species is subject to commercial fisheries, aquaculture, and experimental use (FishBase, 2013). With the introductions of Nile tilapia and Nile perch (*Lates niloticus*) to Lake Victoria, hundreds of species have become extinct there, among them *O. esculentus*, although it may persist in satellite lakes of Lake Victoria. It is listed as Critically Endangered on the IUCN (2013) Red List.

Because tilapias are well known to hybridize among species, especially where *O. niloticus* is introduced into an ecosystem, it seemed likely that *O. esculentus* might have hybridized with introduced *O. niloticus*. Several studies have used different classes of genetic markers to determine whether genetically pure *O. esculentus* populations persist in satellite lakes of Lake Victoria, contributing to identification of units of conservation. Screening random amplified polymorphic DNA (RAPD) markers in seven such populations, Mwanja and Kaufman (1995) concluded that hybridization had occurred in both directions and that no pure stocks of *O. esculentus* remained in these particular systems. Agnese et al. (1999) collected specimens of *O. esculentus* from Lake Kanyaboli, a small lake situated about 20 km from Lake Victoria; both allozyme and microsatellite markers suggested that *O. esculentus* had not hybridized with *O. niloticus*. Angienda et al. (2011) assessed population genetic structure, diversity, and integrity of *O. esculentus* populations in Nyanza Gulf of Lake Victoria as well as three satellite lakes within the Yala swamp near Lake Victoria

by screening mtDNA control region sequences and eight nuclear microsatellite loci. They did not detect mtDNA introgression between *O. esculentus* and *O. niloticus* in Lakes Kanyaboli and Namboyo, but did find low levels of nuclear admixture, primarily from *O. niloticus* to *O. esculentus*. Some genetic signal of *O. esculentus* was found in *O. niloticus* in Lake Sare, where *O. esculentus* is not found, suggesting that *O. esculentus* has been extirpated recently by the *O. niloticus* invasion. *O. esculentus* populations in the respective satellite lakes are significantly genetically isolated from each other, with private mtDNA haplotypes and microsatellite alleles, suggesting that populations should be conserved separately in Lakes Kanyaboli and Namboyo. Mwanja et al. (2012) screened seven remnant populations of *O. esculentus* using RAPD and microsatellite markers. Observation of private RAPD bands and microsatellite alleles for the respective populations indicated small founding stocks or genetic differentiation among remnant populations. Both markers showed that populations of *O. esculentus* coexisting with *O. niloticus* were more variable than populations that were not, implying genetic exchange between the two species where they coexist. The *O. esculentus* populations of lakes Manywa, Kayanja, and Kanyaboli were the most genetically distant from Nile tilapia, and also encountered *O. niloticus* least, if at all, in the wild.

O. esculentus was established in satellite lakes by fisheries managers to protect the species from introduced tilapias and Nile perch. *O. esculentus* is threatened in many of these refugia by hybridization with introduced *O. niloticus* where the two species coexist. The long-term survival of *O. esculentus* will depend upon vigilant protection and nurturing of remnant wild populations against genetic swamping from the introduced Nile tilapia. Further genetic analysis of any remaining satellite lake populations will be needed to identify pure populations of *O. esculentus*, underpinning conservation actions such as habitat conservation and prohibition of culture of Nile tilapia in such systems. Conservation could be advanced by establishment of additional refugium populations in waters devoid of exotic tilapias but within the species' native range; movement of founder stocks should be conducted within but not between sub-regional groupings of the various satellite water bodies around the major waters in order to minimize breakdown of any co-adapted remnant population units (Mwanja et al., 2012).

Redbelly tilapia, *Tilapia zillii* is distributed in Africa and Eurasia from south Morocco, the Niger-Benue system, the Senegal, Sassandra, Bandama, Boubo, Mé, Comoé, Bia, Ogun and Oshun rivers, the Volta system, the Chad-Shari system, the middle Congo River basin, Lakes Albert and Turkana, to the Nile and Jordan systems (FishBase, 2013). Although the species is stocked outside its range for aquatic weed control, only one study has addressed genetic variation of wild populations. Rognon et al. (1996) examined allozyme variation of nine populations from Senegal to the Ivory Coast. Partitioning of total genetic diversity showed that a high proportion was the result of between-population differences. In particular, the three Ivory Coast populations displayed a large genetic distance from the Nilo-Sudanian ones, suggesting several colonization events of the Baoule V region of West Africa by the Nilo-Sudanian ichthyofauna. Studies of *T. zillii* are very incomplete in terms of spatial coverage, screening of the full array of DNA markers available, and consideration of adaptive variation. Much more work will be needed in order to resolve any ESUs within the species.

Species with geographically broad distributions and subspecific taxa. Eleven tilapia species have multiple subspecies, structuring that may correspond more or less well to multiple ESUs. The state of knowledge supporting assessment of ESUs and MUs within these polytypic species varies considerably.

Blackchin tilapia, *Sarotherodon melanotheron* occurs in lagoons and estuaries from Mauritania to Cameroon (FishBase, 2013). Three subspecies are recognized, *S. m. heudelotii*, *S. m. leonensis*, and *S. m. melanotheron*. Studies of morphological, blood protein, and allozyme variation (Pouyaud and Agnese, 1995; Teugels and Hansens, 1995; Adepo-Gourene et al., 1998; Falk et al., 1999, 2000) showed limited variation at the intraspecific level. Falk et al. (2003) screened 21 populations *S. melanotheron* from Senegal to Benin for variation at the mtDNA control region. The results of phylogeographic analyses revealed one monophyletic unit for the species with subdivisions corresponding to the named subspecies, i.e., *S. m. heudelotii* in Senegal, *S. m. leonensis* in Sierra Leone and Liberia, and *S. m. melanotheron* from Ivory Coast to Benin. Populations of these intraspecific taxa did not share mitochondrial haplotypes with other populations, although genetic distances were small. The observed distribution of haplotypes was attributed to long-distance gene flow among populations over the recent past. Using the estimated evolutionary substitution rate of

3.8% per million years, the main lineages of *S. melanotheron* diverged an estimated 900,000 years ago. Our interpretation of Falk et al.'s (2003) results suggests that these lineages represent evolutionary significant units. We further suggest investigation of *S. melanotheron* populations using a wider range of markers and consideration of any adaptive variation. The results of these studies will inform delineation of conservation units and conservation planning.

Nile tilapia, *Oreochromis niloticus* occurs in a wide variety of freshwater habitats like rivers, lakes, sewage canals and irrigation channels. Its native distribution is broad (FishBase, 2013), including coastal rivers of Israel, the Nile basin (including lakes Albert, Edward and Tana), Jebel Marra, Lake Kivu, Lake Tanganyika, Awash River, various Ethiopian lakes, the Omo River system, Lake Turkana, Suguta River and Lake Baringo. In West Africa, its natural distribution covers the Senegal, Gambia, Volta, Niger, Benue and Chad basins. It has been widely introduced for aquaculture purposes, sometimes with subsequent adverse ecological or genetic impacts after introduction, as noted elsewhere in this review. Eight subspecies are recognized, *O. n. baringoensis*, *O. n. cancellatus*, *O. n. eduardianus*, *O. n. filoa*, *O. n. niloticus*, *O. n. sugutae*, *O. n. tana* and *O. n. vulcani* (FishBase 2013). Such a polytypic species presents complexity for assessment of conservation units. Because of the importance of the species for fisheries and aquaculture, however, considerable attention has been paid to patterns of population genetic variation.

Early studies of genetics of wild populations of *O. niloticus* tended to address the validity of the subspecies described by Trewavas (1983), with results of some genetics studies suggesting the need for modifications. For example, Seyoum and Kornfield (1992) used restriction endonuclease analysis of mitochondrial DNA to examine relationships among the seven recognized subspecies. They recommended changes in nomenclature based on concordant results of analyses of molecular character sets. Most importantly, the tilapias of Lake Tana, Ethiopia, previously assigned to *O. n. cancellatus*, were described as *O. n. tana*, a new subspecies. Among the *O. niloticus* samples analyzed by Rognon et al. (1996) were seven wild populations from West Africa. The pattern of differentiation they observed was not congruent with Trawavas, (1983) classification because the population from the Nile clustered with the Lake Turkana one, which had been described as a distinct morphological subspecies, *O. n. vulcani*. To assess this issue further, Rognon et al. (1997) assessed variation of the ND5/6 fragment of mtDNA in two East and four West African samples of *O. niloticus* corresponding to a subset of populations already analyzed for allozyme variation. Their results defined three genotypes; genotypes I and II were found together in eastern populations (Lake Manzala and Lake Turkana), while genotype III was restricted to western populations (Senegal, Niger and Volta rivers). Sequence divergence between eastern and western genotypes suggested long-term isolation of populations in these two geographic regions. Vreven et al. (1998) examined morphometric and allozyme variation of nine natural populations and three cultured strains of *O. niloticus*. Natural populations from West Africa and the Nile, all identified as *O. n. niloticus*, differed significantly; the Nile populations were genetically closer to the Lake Edward population, identified as *O. n. eduardianus*. Taken together, results of these studies suggest that *O. n. niloticus* as defined by Trewavas (1983) and the classifications for East African populations are not completely valid.

Later studies of the population genetics of *O. niloticus* more often addressed range-wide patterns of genetic variation, used newer molecular genetic markers, and addressed conservation issues. Screening allozyme and mitochondrial DNA markers, Agnese et al. (1997) screened wild populations of *O. niloticus* from the major basins (the Senegal, Niger, Volta, Nile, Awash, and Suguta rivers, as well as lakes Chad, Tana, Turkana, Edward and Baringo), representing all subspecies. Their results differed somewhat from those of Trewavas' (1983) nomenclature and earlier molecular genetic studies. Agnese et al.'s (1997) results clustered natural populations into three groups: west African populations (in the Senegal, Niger, Volta, and Chad drainages), Ethiopian Rift populations (Lakes Ziway, Awasa, Koka, and Sodore hot springs in the Awash River), and Nile drainage (Nile, Lakes Tana and Edward) and Kenyan Rift populations (lakes Turkana and Baringo and River Suguta). These observations led the authors to hypothesize that *O. niloticus* originated in the Nile and then independently colonized East and West Africa. Screening nine microsatellite DNA loci across 350 samples from ten natural populations representing four subspecies (*O. n. niloticus*, *O. n. vulcani*, *O. n. cancellatus* and *O. n. filoa*), Bezault et al. (2011) found high genetic differentiation among populations across the Ethiopian, Nilotic and Sudano-Sahelian regions and ichthyofaunal provinces ($R_{ST} = 0.38-0.69$). This result suggested the predominant effect of paleo-geographic events at the

13 Conservation genetics of tilapias: Seeking to define appropriate units for management

macrogeographic scale in defining putative ESUs. In addition, intermediate levels of divergence were found between populations in rivers and lakes within the regions, presumably reflecting relatively recent interruptions of gene flow between hydrographic basins ($R_{ST} = 0.24-0.32$), suggesting different MUs.

Nuclear and mitochondrial DNA polymorphisms in various species of East African *Oreochromis* were screened (Nyingi and Agnese, 2007). In Lake Baringo, Kenya, where only *O. n. baringoensis* is present, alien mtDNA haplotypes were observed, apparently the result of introgressive hybridization with *O. leucostictus*. RAPD polymorphism in *O. niloticus* and *O. esculentus* from different sites around Lake Victoria were studied and it was concluded that both species hybridized (Mwanja and Kaufman, 1995). Aallozyme and mitochondrial DNA polymorphisms in sympatric and allopatric populations of *O. niloticus* and *O. aureus* were compared (Rognon and Guyomard, 2003); while nuclear data were congruent with the morphological identification of the respective species, mtDNA data showed differential introgression of mtDNA from *O. aureus* to *O. niloticus* across the West African area. The corpus of work embodied in all these studies shows that introgressive hybridization poses a risk to some populations of *O. niloticus*.

A considerable body of knowledge exists on molecular and adaptive variation within *O. niloticus*. The species has an exceptional ability to colonize and adapt to a wide range of habitats, ranging from small forest rivers to large drainages and lakes, as well as alkaline pools with hot springs (Trewavas, 1983; Philippart and Ruwet, 1982). For example, the sex determination system of natural populations adapted to three extreme thermal regimes showed thermosensitivity of sex differentiation, with large variations in the intensity of response depending on the parents (Bezault et al., 2007), indicating genotype-environment interactions in sex determination in Nile tilapia. More generally, the description of seven sub-species based on eco-morphology (Trewavas, 1983) largely reflects their adaptive divergence. Taking all the results together, the knowledge base for *O. niloticus* presents a baseline for assessing conservation units for tilapias. Multiple putative ESUs correspond more strongly to bioregions than to subspecies. Bezault et al. (2011) discuss the hypothesis that *O. n. filoa* and *O. n. cancellatus* are differentially adapted ecotypes rather than valid subspecies; whether they constitute ESUs is worthy of more detailed consideration than the data before us can support. Additional ESUs may be detected upon detailed survey; for example, Nyingi et al. (2009) found a unique genetic resource in a recently discovered population from a warm water spring, a tributary of the Lobo Swamp in Kenya that had been overlooked in earlier studies of this species. Observation of genetic differentiation among *O. niloticus* populations within regions supports the existence of multiple MUs within certain ESUs, for example, in the Ethiopian and Nilotic regions. For example, analysis of microsatellite variation among five Egyptian populations of *O. niloticus* (Hassanien and Gilbey, 2005) indicated distinct groups respectively inhabiting the deeper lotic Nile River (Assuit and Cairo), the shallow less lotic Delta lakes (Manzalla and Burullus), and the upstream Nile River (Qena). The economic importance of *O. niloticus* worldwide makes knowledge of its genetic resources pivotal for sustainable use of the species in aquaculture operations through breeding programs (Eknath and Hulata, 2009). Hence, further study of molecular and adaptive differentiation is needed to defensibly define conservation units in *O. niloticus*.

Nine other tilapia species – *O. jipe*, *O. pangani*, *O. placidus*, *O. shiranus*, *O. spilurus*, *O. urolepis*, *S. galilaeus*, *S. nigripinnus*, and *S. tournieri* – have multiple subspecies. However, there have been no assessments of whether recognized subspecies can be related to evolutionarily significant differentiation for purposes of conservation planning. Allele frequency data are available for but one or two populations within four of these species (FishBase, 2013). Conservation status of seven of these species has not been evaluated by IUCN; we note that while the respective species as a whole may be secure, ESUs within them may not be secure. At the species level, *O. jipe* is regarded as Critically Endangered due to overfishing and habitat alteration, and *O. placidus* is rated as Least Concern due to hybridization with *O. niloticus*; whether all ESUs within these species are imperiled is not clear within a species-level assessment. Hence, we recommend that phylogenetic and ESU analyses be conducted for polytypic species and that conservation actions be implemented to address risks to imperiled evolutionary units.

General synthesis

Tilapias are species of global importance to aquaculture and fisheries, and exhibit amazing adaptive differentiation. Despite their practical and intrinsic interest, however, 41 species are regarded as of

conservation concern by the International Union for the Conservation of Nature. As in many piscine taxa, factors driving the decline of tilapias include narrow endemism, negative impacts of introduced species (e.g., predation by Nile perch, competition with Nile tilapia, and introgressive hybridization, most often with Nile tilapia), habitat alteration, pollution, and overfishing. Implementing effective conservation practices is all the more difficult because culture of tilapia is so frequently sought in order to promote food security and economic development. Within this context, Lind et al. (2012) addressed issues pertaining to aquaculture development in Africa, discussing strategies such as zoning, environmental risk analysis, and molecular characterization approaches that can be used to minimize the potential harm to wild fisheries genetic resources arising from aquaculture activities and future development.

Against the background of recent theoretical developments within conservation genetics and applications for salmonid species, we here make the case that focus on conservation of tilapias at the species level underestimates the true level of conservation concern. That is, the concepts of evolutionary significant units and management units largely have not been applied to conservation of tilapias, limiting our ability to define the scientifically most defensible units for conservation planning and implementation. Our review shows that most information on genetic variation, phylogeography, and adaptive variation within species of tilapias is scattered and concentrated on species of aquacultural importance, limiting our ability to assess ESUs and MUs within species solely of conservation concern. While we recognize examples of the work needed [e.g., D'Amato et al. (2007) on *Oreochromis mossambicus*], it is clear that the corpus of work is inadequate to the task at hand, and that the conservation community has much yet to learn. Hence, we advocate study of phylogeography and adaptive variation across the distributional ranges of tilapia species, to provide the basis for informed conservation planning and practice.

Until the task of assessing ESUs and MUs is accomplished for any focal species, conservation biologists would benefit from knowledge and application of any generalities that can be drawn upon for considering provisional conservation units. As shown by our review of the literature for tilapias (e.g., Rognon et al., 1996; D'Amato et al., 2007; Bezault et al., 2011) and other aquatic species, differentiation among ESUs often relates to paleogeographic processes driving drainage boundaries (e.g., tectonic processes), modified in some cases by paleo-events or modern climatic events, e.g., connections by pluvial lakes (e.g., as in *T. zillii* – Rognon et al., 1996) or losses of such connections. Boundaries of many MUs generally will relate to watersheds and standing waterbodies within these major drainages, although because of restricted dispersal capacity for some species, there may be demographically independent units within watersheds and large lakes (Bezault et al., 2011). Until the results of purposeful assessments of ESUs and MUs are in hand, application of best professional judgment is required.

The goal of our review and synthesis study was to summarize knowledge and recommend critical work yet to be done regarding genetic aspects of conservation of tilapias. We hope that our review and synthesis spark critical discussion of tilapia conservation within the tilapia aquaculture, management, and conservation communities.

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19 *Conservation genetics of tilapias: Seeking to define appropriate units for management*

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