

# Chapter 18

## Explosive Speciation and Adaptive Radiation of East African Cichlid Fishes

Christian Sturmbauer, Martin Husemann, and Patrick D. Danley

**Abstract** Cichlid fishes are the most species-rich group of all teleost fishes. Their diversity is centered in the East African Great Lakes where more than 2,000 species evolved within the past 10 million years, representing the fastest vertebrate radiation known. Ongoing molecular phylogenetic analyses indicate that the cichlid radiation originated within Lake Tanganyika. Within the Tanganyikan radiation, seven lineages diversified during the primary radiation to occupy all available freshwater fish niches. The Tanganyikan radiation is the oldest, containing the greatest phenotypic diversity of all East African cichlid radiations, and is ancestral to the cichlid radiations found within Lakes Victoria and Malawi. The radiations in Victoria and Malawi are reciprocally monophyletic and are rooted within the C-lineage of the primary Tanganyikan radiation. While greater numbers of species are found within both Lakes Victoria and Malawi relative to the Tanganyikan radiation, these species flocks have a lower phenotypic diversity relative to the older Tanganyikan radiation. The construction of phylogenetic hypotheses has allowed researchers to explore the extraordinary morphological and behavioral diversity within an evolutionary framework. As a result, the study of cichlids has begun to answer many fundamental questions about the driving forces, mechanisms, and pathways of diversification. These studies demonstrated that cichlid diversification has been influenced by a complex combination of micro-allopatry, natural and sexual selection, facilitated by genetic mechanisms. Here we discuss these patterns, processes, and influences and also point to specific biological conservation problems of cichlid species flocks due to their extreme species richness and restricted species distribution. The current threats are not (yet) caused

---

C. Sturmbauer (✉)

Department of Zoology, Karl-Franzens University of Graz, Universitätsplatz 2, 8010 Graz, Austria  
e-mail: [christian.sturmbauer@uni-graz.at](mailto:christian.sturmbauer@uni-graz.at)

M. Husemann • P.D. Danley

Biology Department, Baylor University, One Bear Place 97388, TX 76798 Waco, USA

by habitat destruction and pollution but by overharvesting. Possible tactics to maintain diversity are proposed.

## 18.1 Introduction

With about 25,000 species formally described, teleost fishes are the most species-rich group of vertebrates. Of these, more than 10% belong to a single family – the Cichlidae. Cichlids have diversified into all imaginable ecological niches in available tropical freshwater systems and stand out as a paradigm for explosive speciation and adaptive radiation. Their multitude of body shapes, specializations, colors, and behaviors is unsurpassed (Boulenger 1898; Fryer and Iles 1972; Greenwood 1973, 1974, 1984a; Barlow 2000; Chakrabarty 2005). Two hundred and twenty genera are currently recognized in FishBase (<http://www.fishbase.org/>). Their natural distribution spans the southern tip of India and Sri Lanka with three species, Madagascar with 47 taxa in five genera ([http://www.cichlid-forum.com/articles/species\\_list\\_madagascar.php](http://www.cichlid-forum.com/articles/species_list_madagascar.php)), Central- and South America with 400–500 species and Africa with probably over 2,500 species. Interestingly, cichlids have not colonized Australia. In accord with the sequence of the split of Gondwana, Indian and Malagasy cichlids form the most ancestral split in the diversification of cichlid fishes, followed by the split between the African and American lineages (Zardoya et al. 1996; Streelman et al. 1998; Farias et al. 1999, 2000; Sparks 2004). Few species managed to move northward into the North American subcontinent (New Mexico and Texas) and into Asia Minor and Asia (Jordan valley and Iran). The maximum evolutionary age of cichlids is thus constrained by vicariance to 130–165 million years and the split between African and American cichlids to about 70–90 million years (Chakrabarty 2004). While riverine ecosystems tend to be relatively species-poor (Katongo et al. 2005, 2007; Koblmüller et al. 2008a) – with the exception of the large South American rivers and perhaps the Zambezi (Joyce et al. 2005) – lakes comprise extremely species-rich communities. Their hotspot of biodiversity clearly lies in the three East African Great Lakes, Victoria, Malawi, and Tanganyika, where an estimate of 1,800–2,000 species, i.e., 60% of the total cichlid diversity, are centered in species flocks (Greenwood 1984a). With a surface area of 68,800 km<sup>2</sup>, Lake Victoria is the largest lake on earth and contains an estimated number of >500 cichlid species (Seehausen 2002). Lake Victoria is not a rift lake and is relatively shallow with a maximum depth of about 80 m. Its maximum geological age has been gauged to be between 250,000 and 750,000 years (Johnson et al. 1996), while the actual age of the species assemblage is a matter of discussion as a dry-up of the lake 17,000–11,700 years ago might have terminated the species flock partially or as a whole (Johnson et al. 1996; Seehausen 2002; Fryer 2004). In terms of monophyly, molecular phylogenetic studies suggested the Lake Victoria haplochromines to be part of a larger phylogenetic lineage of modern haplochromines that are found in several water bodies surrounding the lake including Lakes Albert, Edward, George, Kyoga, and Kivu

and their interconnecting rivers (Meyer et al. 1990; Nagl et al. 2000; Seehausen et al. 2003; Verheyen et al. 2003). Lakes Malawi and Tanganyika are true rift lakes, situated in the East African rift valley between the central and eastern African tectonic plates. Lake Malawi is about 700 m deep and has a tectonic age between 2 and 5 million years (Johnson and Ng'ang'a 1990), with a probable younger age for its species flock due to a late Pleistocene dry-up (Delvaux 1995). Moreover, it experienced two severe reductions in lake level during two East African megadroughts 75,000 and 135,000 years ago (Owen et al. 1990; Scholz et al. 2007), so that several species of rock-dwelling cichlids may be extremely young (Genner et al. 2010). Overall, it contains 500–700 endemic cichlid species (Turner et al. 2001). With a maximum depth of 1,470 m, Lake Tanganyika is the deepest of the three lakes and also the oldest. Its geological age was estimated to be between 9 and 12 million years. Unlike Lake Malawi which consists of a single lake basin, Lake Tanganyika is made up of three basins. The current Lake Tanganyika is likely the product of the fusion of three proto-lakes to a single large lake during its long history (Cohen et al. 1993, 1997). Tanganyika's cichlid assemblage may be younger than the basin(s) themselves, but most likely of an age of 5–6 million years (Koblmüller et al. 2008b; but see Genner et al. 2007). Interestingly, with an estimated total number of 250 endemic species Lake Tanganyika has fewer species than Lakes Malawi and Victoria, albeit their overall degree of eco-morphological divergence is much greater (Greenwood 1984b).

## 18.2 Evolutionary History and Trajectories of Cichlid Fishes

### 18.2.1 *Patterns of Species-Richness in Cichlid Lineages*

Previous molecular phylogenetic work suggested reciprocal monophyly of the extant African and South American cichlid lineages (Streelman et al. 1998; Sides and Lydeard 2000), rejecting the morphology-based placement of the African genus *Heterochromis* at the base of the South American cichlids (Kullander 1998). Within Africa, several lineages diversified at an early stage, many of them being restricted to particular biogeographic regions. The tribe Tilapiini (>88 species) is one of the two large African cichlid taxonomic units defined on morphological grounds (Greenwood 1984b; Eccles and Trewavas 1989). However, the Tilapiini turned out to be a conglomerate of several lineages (Klett and Meyer 2002), scattered among the remaining ancestral splits. The haplochromine cichlids turned out to be (almost) monophyletic, with a highly intriguing evolutionary history. Thus, the diversification of the tilapiine cichlids coincided with that of other ancestral African lineages, predating the African rifting processes, while that of the haplochromine lineage coincided with and in fact was tied into the very first wave of adaptive radiation triggered by the rifting process in East Africa, in the proto-lake(s) of Lake Tanganyika.

The species inventories of rivers and lakes clearly suggest that large lakes are the centers of diversity, while riverine faunas are relatively species-poor and less dominated by cichlid fishes (Fryer and Iles 1972). Diversification in riverine environments seems to be driven by range expansion, colonization by river capture and subsequent geographic isolation, so that vicariant and geographic speciation best explains the modest diversity of riverine cichlids throughout the world (Joyce et al. 2005; Katongo et al. 2005, 2007), with the few exceptions mentioned above. Small lakes are often shallow and swampy with papyrus reeds surrounding them and mostly contain few species (see Fig. 18.4 in Salzburger and Meyer 2004). For example, the shallow Lake Kanyaboli, a satellite of Lake Victoria harbors just seven haplochromine and two tilapiine species, of which only one or two are endemic (Odhiambo et al. 2011). Mayr (1942) already observed that species number correlates with lake size rather than age and suggested that the much higher number of ecological niches and/or the higher potential for spatial separation due to long shoreline facilitates the intralacustrine allopatric speciation (see also Barluenga and Meyer 2004). The enormous diversity and impressive endemism rates in large East African lakes suggest intralacustrine speciation as the most common mode of diversification. Seehausen (2006) counted 27 lacustrine cichlid radiations in Africa. In all these lakes, cichlid fish invariably form the most species-rich teleost lineage. Cichlids consistently out-compete other fish groups when colonizing a newly emerging lacustrine ecosystem and in doing so, the species flocks ecologically diversify and occupy a range of niches. For these reasons, cichlid fishes represent an excellent model system to study adaptive radiation: the process of extremely rapid species formation coupled with ecological, morphological, and behavioral diversification.

The theory of adaptive radiation requires two conditions to be met (1) the formation of a new habitat or a dramatic change of an already existing habitat and (2) the possession of a so-called key innovation, a set of traits allowing for rapid adaptation to novel niches. Thus, one feature or a certain set of features allows one group to outcompete the other taxa, thereby giving rise to an abundance of monophyletic species. In the case of East African lakes, several teleost groups had the same chance to colonize the newly emerged lakes: cyprinids, characins, mormyrids, various catfish, sardines, Nile perches, and spiny eels; but judging from endemism rates, only cichlids underwent major diversification. Such that while Lake Tanganyika contains four endemic Nile perch species, six catfishes, six spiny eels, and two sardines, 90% of the fish in Lake Tanganyika are endemic cichlids. In the case of cichlid fishes, the key innovation may be a highly effective combination of factors. The first concerns trophic morphology; cichlids possess two sets of jaws, a characteristic shared with other labrid families (Liem 1973; Mabuchi et al. 2007). The oral jaws have specialized for food acquisition and manipulation. A hydrodynamic tongue then passes captured food items to the pharyngeal jaws (Liem 1991). The pharyngeal jaws are formed by parts of the gill arches, are connected to the neurocranium via the pharyngeal apophysis and process food in a wide variety of ways before swallowing. Both jaws have evolved to realize diverse foraging strategies: Cichlid oral jaws can catch fish, shrimp, or insects,

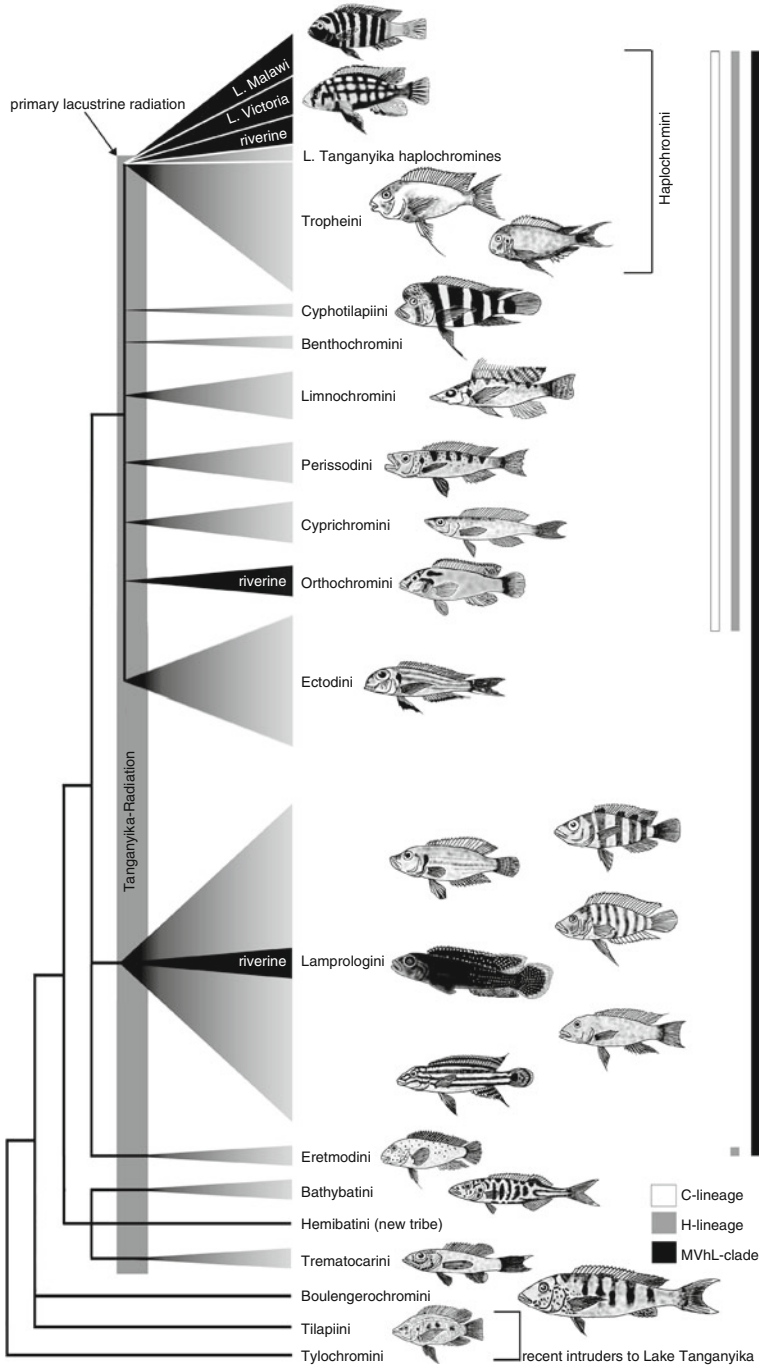
browse filamentous algae from rocks, comb off unicellular algae and detritus from algal bio-mats, and even bite off fish scales from other cichlid species. Pharyngeal jaws can macerate food items, crush gastropod shells, slice off tissue or staple fish scales before swallowing. Allometric changes of these structures together with modifications of other body parts enable cichlids to efficiently adapt to novel food niches, without the need of de novo evolution of anatomical features (Stiassny 1991; Albertson et al. 1999; Clabaut et al. 2007).

The second outstanding feature of cichlids concerns their efficient brood care (Fryer and Iles 1972). Ancestral lineages are substrate breeders from which several groups branched off by independently shifting to various ways of mouthbrooding, i.e., incubating eggs and/or fry in the buccal cavity (Goodwin et al. 1998; Stiassny and Meyer 1999). Both breeding modes involve territorial behavior and facilitate raising the young in densely packed communities. Concerning species diversity, all East African lakes except for Lake Tanganyika exclusively comprise maternal mouthbrooders of the haplochromine cichlid lineage. Only Tanganyika contains a sub-flock of the substrate-breeding lamprologine lineage, together with a variety of lineages with various styles of mouthbrooding. This diversity is the result of the multiple independent evolution of mouthbrooding in the course of the Tanganyikan radiation, which seeded the most species-rich lineage, the haplochromines. The haplochromines appear to have left the Tanganyikan proto-lake at an early stage to colonize several other water bodies (Salzburger et al. 2002b, 2005; Verheyen et al. 2003; Clabaut et al. 2005; Koblmüller et al. 2008b).

### 18.2.2 The “Out of Tanganyika Hypothesis”

Lake Tanganyika is the second-oldest lake in the world and was the first major water body formed during the East African rifting process. It has a highly complex geological history (Scholz and Rosendahl 1988; Gasse et al. 1989; Tiercelin and Mondeguer 1991; Cohen et al. 1993, 1997; Lezzar et al. 1996; Scholz et al. 2003). Seven lineages of cichlids colonized the emerging Tanganyikan proto-lake(s) and seeded the so-called “primary lacustrine radiation” (Salzburger et al. 2002b; Fig. 18.1). Cumulative molecular phylogenetic evidence suggests that this diversification event coincided with the establishment of deep-water conditions in a clear lacustrine habitat about 5–6 million years ago (Tiercelin and Mondeguer 1991; Cohen et al. 1993, 1997). This timeframe suggests that the Tanganyika radiation did not happen at the earliest stage of lake formation, dated at 9–11 million years ago, when the rifting process slowed down the Proto-Malagarazi-Congo River to form a series of shallow and swampy proto-lakes, interconnected by a meandering river network (Sturmbauer 1998). While the vast majority of species was not formed in these early swampy proto-lakes, this period in the Tanganyikan radiation was likely important in the divergence of the seeding lineages.

The seven seeding lineages were the ancestors of the substrate-breeding predator *Boulengerochromis microlepis*, the genus *Hemibates*, and of the Bathybatini,



**Fig. 18.1** Schematic molecular phylogenetic tree of the Lake Tanganyika cichlid species assemblage, and its relationships to the species flocks of Lakes Malawi and Tanganyika, based upon

Trematocarini, Eretmodini, Lamprologini, as well as of the C-lineage (sensu Clabaut et al. 2005). Molecular phylogenetic studies further demonstrated that *Oreochromis tanganyicae* and *Tylochromis microlepis* had not yet been present in the lake at the time of the primary radiation, but had colonized the lake more recently (Klett and Meyer 2002; Koch et al. 2008). In the course of the “primary lacustrine radiation,” the substrate-breeding Lamprologini and the mouthbrooding C-lineage diversified rapidly into several new lineages (Salzburger et al. 2002b; Takahashi and Okada 2002; Terai et al. 2003; Clabaut et al. 2005; Sugawara et al. 2005). Mitochondrial DNA data suggest that haplochromine cichlids represent a paraphyletic assemblage, in that the *Orthochromis* species which are presently distributed in the Malagarazi River system, originated independently from the remaining haplochromines in the course of the “primary lacustrine radiation” (Salzburger et al. 2002b, 2005), but ancient incomplete lineage sorting may be an alternative explanation (Takahashi et al. 2001). Interestingly, the genus *Hemibates*, which was originally considered as a member of the Bathybatini, split from the ancestors of the large *Bathybates* species and the Trematocarini prior to the “primary lacustrine radiation” (Koblmüller et al. 2005).

Of the seeding lineages, two lineages, the Lamprologini and the C-lineage, underwent major diversification through successive divergence events. Both lineages gave rise to species that left the lake to colonize surrounding rivers (Salzburger et al. 2002b). Substrate-breeding lamprologine cichlids are found in the Lower Congo and the Malagarazi River, and haplochromine cichlids are found almost throughout Africa. In each of the newly colonized systems, both lineages further diversified.

The haplochromines consist of six lineages which originated within a short period of time, about 5.3–4.4 million years ago (Koblmüller et al. 2008b). They show a highly complex phylogeographic pattern, carrying the signature of climate- or geology-induced changes of the environment, with river capture due to tectonic tilting playing an important role for species dispersal across major drainage systems. The first lineage comprises only one species from southeastern Tanzania, *Haplochromis pectoralis*. The second lineage contains the eastern African genus

←

**Fig. 18.1** (continued) combined evidence from several studies. Lineages that underwent radiation are indicated by triangles, whose size corresponds to the species number within these lineages (except for *triangles* symbolizing the riverine ancestors and the species flocks in Lake Malawi and Lake Victoria). *Black triangles* indicate lineages that do not occur in Lake Tanganyika. The “primary lacustrine radiation” (Salzburger et al. 2002b) is assumed to have coincided with the establishment of a true lacustrine tropical habitat with deepwater conditions about 5–6 million years ago. *Bars to the right* indicate taxonomic groups that have been proposed based upon combined mitochondrial and nuclear DNA data (C-lineage; Clabaut et al. 2005), allozyme data (H-lineage; Nishida 1991), and SINEs (MVhL-lineage; Takahashi et al. 2001). Note that the phylogenetic history of most tribes is much better resolved and that branch lengths and proportional times of radiation are not to be taken as accurate. Tribes are named according to Takahashi (2003) and Koblmüller et al. (2008b), with the exception for the suggested new tribe for *Ctenochromis benthicola* which turns out as close relative of the genus *Cyphotilapia* (Walter Salzburger, unpublished results)

*Astatoreochromis* with three species. The third lineage is represented by a single undescribed species, so far only found in the upper Lufubu River. The fourth lineage contains the genus *Pseudocrenilabrus* with a wide distribution all over eastern-, central-, and southern Africa. Lineage five represents the so-called modern haplochromines and lineage six, the *Serranochromis*-like cichlids, has its center of diversity in Central- and southern Africa. The modern haplochromines and the *Serranochromis*-like cichlids both have a wide and complementary distribution.

In terms of species richness, species flocks have been found in three clades: the *Pseudocrenilabrus* clade with a small species flock in Lake Mweru (Katongo and Seehausen, personal communication), the Serranochromines with a now riverine species flock that might have originated in Paleo-Lake Makgadikgadi (Joyce et al. 2005) or in another water body in this area (Frank Riedel, personal communication), and the modern haplochromines with maybe close to 2,000 species in about 25 lacustrine species flocks.

The endemic Lake Tanganyika tribe Tropheini is the sister group of the modern haplochromines. Their split from the remaining modern haplochromines was dated at 3.4 (3.0–4.0) million years ago. It is thought that the Tropheini originated in Lake Tanganyika, almost simultaneously with the remaining Tanganyikan mouth-brooding lineages, typical of lacustrine radiations but unusual for riverine assemblages (Joyce et al. 2005). However, it has been suggested that the riverine ancestor of the Tropheini re-entered Tanganyika and then subsequently radiated into several niches of predominantly rocky habitats (Salzburger et al. 2005).

The riverine haplochromines related to the Tropheini colonized Lakes Malawi and Victoria. At least one species of the Tropheini, *Ctenochromis hoorii*, also inhabits inflowing rivers and overlaps with *Astatotilapia burtoni*, the sister group of the Lake Victoria superflock. This sister group relationship is also supported geographically (Koblmüller et al. 2008b; Verheyen et al. 2003). Given that an undescribed modern haplochromine from the oasis El Fayoum in northern Egypt as well as *Haplochromis flavijosephi* from the Jordan Valley, nested within the East African clade (Werner and Mokady 2004), a Pleistocene dispersal along the Nile was suggested. Another lineage of modern haplochromines comprising the *Astatotilapia bloyeti* species complex colonized the more southern Tanzanian water bodies and seeded the Lake Malawi species flock. That said, it becomes evident that despite being independent radiations, the East African lacustrine haplochromines are connected by riverine species and root within the Lake Tanganyika Tropheini radiation.

### ***18.2.3 Models of Adaptive Radiation***

The tremendous diversity in East African lakes inspired the first evolutionary biologists who studied these systems to invoke novel modes of speciation involving sympatric mechanisms. The term scizotypic speciation was coined by Woltereck (1931) for Wallacean decapods and rapidly adopted to the cichlid speciation



problem (Rensch 1933; Kosswig 1947; Brooks 1950). However, little progress was made towards a better understanding of the processes involved until the mid-eighties, as summarized by Ernst Mayr (1984). However, many issues plagued our understanding of the cichlid evolutionary history at that time: the age of the lakes and their species assemblages were unknown, taxonomic problems remained, and there was an almost complete lack of phylogenetic hypotheses. Nonetheless, three factors were recognized contributing to the extreme species richness of these systems: multiple colonization, fusion of several proto-lakes, and intralacustrine speciation (Mayr 1984).

Aside from geological processes, lake level fluctuations were recognized as an additional powerful promoter of intralacustrine allopatric speciation. Rossiter (1995) later termed this as “species pump speciation,” in recognition that most cichlids are highly philopatric and restricted to particular types of shore substrate (Mayr 1984). Speciation was tied to the biological species concept of Mayr (1942, 1947) invoking the evolution of isolating mechanisms as barriers to gene flow that were thought to predominantly evolve in allopatric phases. Fine-scale geographic structure was recognized by Mayr as potential basis for microallopatric speciation. Speciation in connection to niche divergence, however, was questioned by him as being unlikely given the slight differences among incipient species. This opinion has changed in recent years and researchers now have a more differentiated view about the driving forces of speciation.

Speciation driven by (divergent) natural selection, termed ecological speciation, has been put forward as one major factor accounting for cichlid diversity (Schluter 1996; McKinnon et al. 2004). By comparing the overall degree of morphological divergence found within the three great East African lakes, Greenwood (1984b) concluded that species with similar morphologies would be characteristic in evolutionarily younger flocks, while highly diversified species would point to an older evolutionary age. These observations suggest that morphological diversification is driven by natural selection which continues to push morphologies towards more and more extreme forms (Mayr 1984). A second factor, sexual selection via mate choice, was brought up as a potentially powerful driving force (Dominey 1984), particularly in maternal mouthbrooders. Dominey’s conceptual paper seeded a novel realm of research on sexual selection via female mate choice (Turner and Burrows 1995; Knight et al. 1998; Seehausen and Van Alphen 1999; Seehausen 2000). Moreover, the dominance of allopatric speciation was also questioned in particular phases of a radiation, and it was recognized that both natural and sexual selection have the potential to act in sympatric and allopatric situations (Sturmbauer 1998).

To reconstruct and understand the radiation pathways, knowledge of the geological and biogeographic history of the lake in question is needed to identify the probable source of seeding species. Then a phylogenetic hypothesis for the species flock is needed, based upon ecological, morphological, behavioral, and genetic data (Stepien and Kocher 1997). Finally, the modulators triggering speciation and ecomorphological diversification at each stage must be identified. Conceptual progress was made towards a better understanding of more large-scale patterns of the radiation process (Mayr 1984; Greenwood 1984b; Coulter 1991; Meyer 1993;

Schluter and McPhail 1993; Martens et al. 1994; Kornfield and Smith 2000; Schluter 2000; Turner 2007), and the stages of adaptive radiation progresses (Sturmbauer 1998; Danley and Kocher 2001; Streelman and Danley 2003). Radiations become adaptive by the tight coupling of fast speciation rates and eco-morphological and/or behavioral diversification. When natural selection is involved, speciation events show a “niche divergence first – speciation later” pattern, in turn, when sexual selection is the prime driving force, a “speciation first – divergence later” pattern emerges. The relative importance of the factors driving the whole process shifts with time; adaptive radiation must be viewed as an interactive process with a self-generated shift of abiotic and organismic modulators (Sturmbauer 1998).

The initial stage of cichlid adaptive radiation is characterized by riverine colonizers. Such species are generalists, able to cope with a seasonally fluctuating environment, and capable to colonize a variety of lake habitats still free from more specialized competitors. Accordingly, the first speciation events are tied to the colonization of major habitats such as rocks, sand bottom and the pelagic zone (Danley and Kocher 2001), so that the first emerging species adapt to “fundamental niches,” possibly via sympatric mechanisms given the great dispersal ability of generalist colonizers (Sturmbauer 1998). Data from several systems suggest that this to be a common trend in vertebrate radiations (Streelman and Danley 2003). Lake Malawi, for example, was colonized by a generalized cichlid that first diverged into two major clades, the rock-dwelling mbuna and a sand-dwelling clade, plus several other oligotrophic lineages (Moran et al. 1994; Danley and Kocher 2001). The polyphyletic Lake Tanganyika radiation proceeded in a similar fashion, in that each diversifying lineage seems to have picked one habitat type and fundamental niche. Tilapiine cichlids in a West African crater lake (Schliewen et al. 1994, 2001; Schliewen and Klee 2004) and Heroine cichlids in the Central American Lake Apoyo (Barluenga et al. 2006) also follow the “major habitat first” rule.

The second phase of diversification results from the subdivision of fundamental niches. Within each fundamental niche, species emerge through the modification and refinement of the trophic apparatus. As a result, lineages which diverged during this phase can be distinguished based on trophic structures, feeding behavior, and diet. Such adaptations to the partitioned macrohabitat may further reduce gene flow thereby facilitating species divergence (Sturmbauer 1998). This pattern can be found in both Lake Malawi and Tanganyika cichlid lineages (Albertson et al. 1999; Sturmbauer and Meyer 1993; Sturmbauer et al. 2003; Salzburger et al. 2002b; Koblmüller et al. 2004, 2005, 2007a, b, c; Duftner et al. 2005; Brandstätter et al. 2005) and seems to be general for aquatic and terrestrial vertebrates (Streelman and Danley 2003).

A third phase of radiation promotes the divergence of reproductive characters without large eco-morphological change. During this phase, speciation seems to be primarily driven by sexual selection on male mating-relevant traits, such as male signaling phenotypes. This process is evident many species-rich radiations, such as the Victorian and Malawian haplochromine radiations, but is not wide spread in the relatively species poor Tanganyikan (Streelman and Danley 2003).

## 18.3 Factors Driving Divergence

### 18.3.1 (*Micro-*) *Allopatry and Reduced Gene Flow*

Geographic separation and extrinsically reduced gene flow are thought to be of primary importance in the majority of speciation events (Mayr 1942). In East African lacustrine cichlids, allopatric divergence is thought to have occurred through large lake level fluctuations, which split Lake Tanganyika into separate basins (Sturmbauer et al. 2001) and has isolated satellite lakes from the main lake basins of Lakes Malawi and Victoria (Brooks 1950; Greenwood 1965; Genner et al. 2007).

While the type of large-scale vicariance events common in other systems have played a role in the evolution of East African cichlids, the reduction of gene flow in these can occur over much shorter geographical scales and in the absence of major geologic events typically associated with divergence via vicariance. Many studies demonstrated between-population differentiation across as little as 2–5 km (Kornfield 1978; Van Oppen et al. 1997; Danley et al. 2000; Rico and Turner 2002; Smith and Kornfield 2002; Duftner et al. 2006; Koblmüller et al. 2007c; Sefc et al. 2007; Streebman et al. 2007; Wagner and McCune 2009). As a result, many East African cichlid species are “narrow endemics” often only present on a single stretch of continuous habitat (Ribbink et al. 1983). Furthermore, the shoreline of Lakes Malawi and Tanganyika consist of a patchwork of sandy and rocky habitats. This, and the extreme territoriality of most members of the Tropheini and Haplochromini, suggest that no large geographic distances or barriers are needed to reduce gene flow between populations living in neighboring habitat patches. The extreme philopatry, maternal mouthbrooding, and lack of dispersal during any life stage create circumstances in which microallopatric divergence can occur on the order of kilometers (Sturmbauer and Meyer 1992; Verheyen et al. 1996; Van Oppen et al. 1997; Arnegard et al. 1999; Markert et al. 1999; Danley et al. 2000; Salzburger et al. 2005). The low gene flow between neighboring populations suggests that even weakly differentiated selective environments could lead to the fixation of characters within local populations (Danley et al. 2000).

### 18.3.2 *Localized Adaptation*

The reduction of gene flow can lead to independent evolutionary trajectories. Different localities may comprise varying environmental conditions and selective pressures; these may involve factors such as rock size, inclination, wave exposure, food availability, and predation pressure. In addition, light environment, water turbidity, and other parameters influencing mate recognition may vary among sites and likely influence intensity and direction of sexual selection (Seehausen et al. 1997). Hence, local adaptation can be driven by natural as well as by sexual

selection, and indeed, population differences have been found in trophic characters (e.g., Streebman et al. 2007; Herler et al. 2010) and mate choice traits (e.g., Maan et al. 2004).

### 18.3.3 Sexual Selection

Dominey (1984) was among the first to convincingly argue that sexual selection had a major influence on cichlid diversification. Since then sexual selection has been implicated in the divergence of a wide variety of phenotypes including brain size (Gonzales-Voyer et al. 2009), cooperative behavior (Bruitjes and Taborsky 2008), and territorial behavior (Markert and Arnegard 2007). Male nuptial coloration is the most widely studied target of sexual selection. The diversification in hue and color pattern is obvious and widespread particularly in the maternally mouthbrooding cichlids. Furthermore, diversity in color pattern is one of the most easily identified phenotypes by the human sensory system. However, recent evidence suggests that visual cues alone are not always sufficient for accurate mate discrimination. Mate recognition systems likely include visual, acoustic, and chemical characters. Recently, it has been suggested that selection on multiple cues might accelerate speciation rates, and different communication systems might act in close association with each other (Blais et al. 2009; Smith and Van Staaden 2009). Here, we review the different communication systems on which sexual selection may act and their impact on reproductive isolation and speciation.

#### 18.3.3.1 Vision

Most research on communication in cichlids has concentrated on visual cues. This is easy to understand if one regards the great conspicuous diversity of male breeding coloration. Different aspects of morphology and coloration have been shown to ensure assortative mating and hence prevent hybridization (Seehausen et al. 1997; Seehausen and van Alphen 1998; Blais et al. 2009).

#### Body Size

Schliwen et al. (2001) found strong size-assortative mating in two sister species of cichlids in a lake in Cameroon. A study by Baldauf et al. (2009) revealed preferences for larger mates of both sexes in the West African cichlid *Pelvicachromis taeniatus*. Seehausen and van Alphen (1998) suggested that body size can be a mate choice signal when color is not available. Also, indirectly selection may act on body size. In some species, larger males are able to acquire larger or higher quality territories which are preferred by females (Markert and Arnegard 2007).

## Color Pattern and Hue

East African cichlid fishes are well known for their amazing variety of color morphs. Typically, both males and females of a given species can be distinguished from sympatric species based on color pattern. However, female color patterns are generally dull and are believed to confer some degree of crypsis. In contrast, males, particularly those of the rock-dwelling cichlids, are conspicuously bright. Because male color pattern is so easily distinguished by the human sensory system, it is the most widely studied character believed to be under sexual selection.

Male nuptial coloration and female mate choice are known to contribute to assortative mating and reproductive isolation in many cichlid species (Coultrige and Alexander 2002; Jordan et al. 2003; Venesky et al. 2005). Stelkens and Seehausen (2009) found that phenotypic divergence, including nuptial coloration, is a better predictor for reproductive isolation than genetic distance for a closely related group of East African cichlids. Mate choice experiments using different light environments and field studies suggested that hue might be the most important cue used for mate evaluation (e.g., Seehausen et al. 1997; Seehausen and van Alphen 1998; van Oppen et al. 1998; Streelman et al. 2004; Maan et al. 2010). Other studies suggest that color pattern is the most important visual cue (e.g., Coultrige and Alexander 2002; Jordan et al. 2003; Stelkens et al. 2008). The final evaluation of each cue remains and present knowledge suggests that a combination of both color and hue might be decisive for mate choice.

While much work has been done to describe the role that color pattern and hue play in mate recognition and sexual selection, only recent studies have begun to address the causative factors involved in their evolution. Seehausen and colleagues (2008) provide the most comprehensive and insightful examination female preference and male hue evolution to date. This work examines the sensory drive hypothesis along an environmental transect in Lake Victoria. In their exhaustive study, the authors demonstrate correlated changes in male color pattern, frequencies of opsin alleles with differing sensitivities, female mate preference for male hue, and ambient light along an environmental gradient. This study examined the crucial links between female preferences, visual physiology, and the environment and in doing so provides one of the most comprehensive explanations of male color pattern and female mate choice diversity in cichlid fishes.

Females are not the only sex to exhibit mating preferences based on color patterns. Males also exhibit mating preferences for sex-linked female color patterns. This preference appears to be inherited and may contribute to formation of new species (Pierotti et al. 2008). However, male mating preferences vary considerably within populations indicating high dynamics of this trait (Pierotti et al. 2008). Additionally, natural selection may limit the divergence of coloration due to its role in camouflage and adaptation to habitat (Salzburger 2009).

## Sand Bowers

Males of sand dwelling cichlids often build sand bowers which are used to attract females. These bowers represent extended male visual phenotypes which are of species-specific size and shape (McKaye et al. 1990; McKaye et al. 1993; Rossiter and Yamagishi 1997; Stauffer et al. 2002; Kidd et al. 2006). These bowers are solely used as display sites to attract females (McKaye et al. 1990; Tweedle et al. 1998) which prefer conspecific bower shapes. Hence, this character has the potential to cause reproductive isolation among closely related sand-dwellers (McKaye et al. 1993). Often bowers of numerous males are organized in leks, where males display to passing females (Tweedle et al. 1998). Females move over the lek and mate with several males (McKaye 1991; Stauffer et al. 2002).

Studies suggest that female mate choice shapes the bower architecture. For example, in a number of species, males with taller bowers have higher breeding success (McKaye et al. 1990; Stauffer et al. 2005). Young et al. (2009) tested for a model explaining lek formation and found support for the “female preference” model. This model predicts that females prefer mating with males which are aggregated in clusters, because of a reduction of predation risk, easier male comparison (more males, shorter distances), and higher quality of lek forming males. Males experience a higher per capita female encounter rate with increasing lek size. Hence, both sexes benefit from lek formation. Yet, nothing is known about the genetic basis and heritability of bower formation and preference (Kidd et al. 2006).

### 18.3.3.2 Non-visual Cues

Recent evidence suggests that visual communication is insufficient to explain the diversity of East African cichlids and the maintenance of species boundaries among closely related species (Plenderleith et al. 2005; Blais et al. 2009). Consequently, additional cues such as olfaction and acoustic signaling have been suggested to play an important role in mate choice (Robinson et al. 1998; Knight and Turner 1999; Amorim et al. 2003; Amorim et al. 2004; Plenderleith et al. 2005; Cole and Stacey 2006; Blais et al. 2009).

#### Acoustic Communication

Studies of cichlid sound production have shown that cichlids employ acoustic communication in a variety of social interactions (Lobel 1998; Nelissen 1978; Ripley and Lobel 2004; Amorim et al. 2003, 2004, 2008; Simões et al. 2006, 2008; Danley et al., unpublished). Acoustic signals may be used for the identification of conspecific mates and the evaluation of male quality (Simões et al. 2008). Acoustic signals are also employed by males (Amorim et al. 2003; Amorim and Almada 2005; Simões et al. 2008; Longrie et al. 2008) and females (Simões et al. 2008) during antagonistic interactions. These observations are in accordance with

the use of acoustic signals in a wide array of other fish taxa (Lobel 1992; Kihlslinger and Klimley 2002; Amorim 2006 for reviews). A recent study identified differences in various acoustic parameters among closely related species of rock-dwelling cichlids and even geographic differences within species suggesting the presence of local acoustic dialects (Danley et al., unpublished). Variation in acoustic signals has already been demonstrated in the whitetail shiner, *Cyprinella galactura* (Phillips and Johnston 2008). However, future studies need to evaluate the within and between population divergence of sound parameters and the importance of this variability in the mate recognition systems of these species.

### Chemical Communication

Chemical communication in cichlid fish is a little explored area. However, previous studies suggest that olfaction is used in a variety of social contexts; females may employ olfactory cues to identify conspecific males (Plenderleith et al. 2005), and olfaction maybe used for the recognition of conspecifics in general (Giaquinto and Volpato 1997). Furthermore, olfactory cues emitted with urine appear to be important social signals and can indicate social status (Almeida et al. 2005; Barata et al. 2007, 2008). The use of electro-olfactograms (EOG) indicates that steroid hormones or steroid-like compounds may be the functional components in urine (Cole and Stacey 2006; Frade et al. 2002; Barata et al. 2008). The importance of chemical cues in cichlid communication is not universally supported; work by Jordan et al. (2003) and Venesky et al. (2005) rejected olfaction as important mate choice cue for Lake Malawi rock-dwellers.

#### 18.3.3.3 Multimodality of Premating Cues

This review of cichlid communication and mate choice suggests that single traits alone are not sufficient to explain the species diversity and maintenance of reproductive isolation (Plenderleith et al. 2005; Blais et al. 2009). More likely, various communication modalities may act in different situations during mating or over different distances. Smith and van Staaden (2009), for example, showed that visual and acoustic communication modalities are associated; the same is probably true for olfaction, and combinations of all cues, but this remains to be tested.

It has been suggested that species richness is a function of the number of traits involved in diversification (Nosil and Harmon 2009). Likewise, Galis and Metz (1998) stated that “a large number of independent elements increases the number of potential solutions for a particular . . . problem.” They used this argument as hypothesis for the tremendous diversity of jaw morphologies, but the same may apply for mating systems. Hence, involvement of multiple communication systems, such as vision, olfaction, and acoustics, would allow for a greater number of taxa. Each of those traits can comprise multiple modalities itself. Visual traits, for example, can be subdivided into shape, pattern, and hue, whereas different acoustic parameters,

including frequency, trill period and pulse period could serve different functions for mate recognition. Furthermore, species may vary in the relative importance of different modalities. For example, cichlids living at great depths in relatively poor photic environments may rely on acoustic and olfactory cues to a greater degree than species living in shallow in-shore areas of the lakes. The multimodal nature of mate recognition and evaluation within cichlids provides a greater phenotypic space for mating signals to diversify, potentially contributing to the high observed diversity of cichlid fishes.

### ***18.3.4 Genetic Factors Influencing Speed and Richness of Divergence***

#### **18.3.4.1 Retention of Ancestral Polymorphisms**

The large amount of shared genetic variation found within the East African species flocks has both fascinated and stymied evolutionary biologists. While Lake Tanganyika species tend to be reciprocally monophyletic using mtDNA (Sturmbauer and Meyer 1992; Sturmbauer et al. 2003), the younger Lake Victoria and Malawi cichlids share mtDNA haplotypes among species (Meyer et al. 1990; Moran and Kornfield 1993). Limited success has been achieved in resolving some clades in these systems using a nuclear genomic multilocus marker system (AFLP) (Albertson et al. 1999; Koblmüller et al. 2007b; Koblmüller et al. 2008b); still, the majority of relationships within the haplochromine cichlids remain unresolved. The use of single nucleotide polymorphisms (SNP) may provide additional resolution. However, a study performed by Loh et al. (2008) suggests that shared polymorphism at SNP loci is also common. Historically, the high level of shared genetic diversity has been attributed to the very recent age of the Lake Malawi diversification, the lack of fixation of neutral markers, and, consequently, the retention of ancestral polymorphism (Moran and Kornfield 1993). More recent studies have focused on the role that hybridization may play in preventing the fixation of alleles within a lineage.

#### **18.3.4.2 Hybridization**

Hybridization has long been thought to slow down evolutionary change (Seehausen et al. 1997). More recent evidence suggests that hybridization could contribute to the evolution of phenotypic novelty, increase genetic diversity within species (Rüber et al. 2001; Salzburger et al. 2002a; Seehausen 2004) and possibly contribute to the creation of new species by introducing new genetic variation in the hybrid population (Albertson and Kocher 2006; Koblmüller et al. 2007b). It was also argued that hybridization may produce more fit individuals via transgressive



segregation, especially if newly formed species possess alternative alleles that are not yet fixed (Seehausen 2004; Bell and Travis 2005; Rieseberg 1999). Traits under strong directional selection, however, are likely to be fixed for alternative alleles. Strong directional selection may limit the degree to which novel phenotypes are produced by hybridization (Albertson and Kocher 2005). However, Parnell et al. (2008) argue that the phenotypic limitations imposed by genetic architecture can be overcome in hybrids even in the presence of strong directional selection. These authors argue against measuring individual morphological elements and for viewing the phenotype as a functional unit that can be arrived at through multiple mechanisms. As an example, they discuss various ways in which the components of the jaw can be structured to produce similar kinematic transmission of the oral jaws. The importance of hybridization in generating genetic and phenotypic novelty is becoming more widely recognized in cichlids and other systems.

#### 18.3.4.3 Gene/Genome Duplication

Gene duplication, whether at the gene or genome scale, makes one of the copied regions redundant and therefore reduces the strength of selection on one of the duplicates. One or both of the copies, therefore, can evolve to take on a more specialized function (subfunctionalization) or may even acquire a new function (neofunctionalization). As a result, gene (or genome) duplication may lead to phenotypic divergence (Ohno 1970). Some authors have suggested that the diverse color patterns seen in East African cichlids, which have been implicated in their extraordinary divergence, may be the result of gene duplications. Within cichlids Watanabe et al. (2007) identified a gene duplication event of *kir7.1*, an inwards rectifier potassium channel that is known to influence zebrafish color pattern. However, the function of *kir7.1* in cichlids remains unknown since the cichlid paralogs (*cikir7.1* and *cikir7.2*) do not appear to be expressed in zebrafish (Watanabe et al. 2007). The duplication of *kir7.1* is only one of many genes involved in pigmentation that have been duplicated in bony fishes. As noted by Braasch et al. (2006), bony fish have duplicates of the pigmentation genes *mitf*, *sox10*, *tryrosinase*, *csflr*, *pdgfrb*, and *kit* (Braasch et al. 2006 and references therein). Braasch et al. (2006) suggest that the fish-specific genome duplication (FSGD) event led to the duplication and neofunctionalization of two physically linked type III receptor tyrosine kinases (RTKs) known to influence vertebrate color patterns. One paralog appears to have retained its traditional function, while the other appears to have taken on a novel function. The authors conclude that genome duplications, including the FSGD event, contributed to increased number of pigment cell types in fishes (Braasch et al. 2006).

Possibly one of the best studied examples of gene duplication involvement in the evolution of phenotypic novelty, and species divergence has been discovered through studying the duplication of opsin genes. Five opsin gene types are found in many vertebrates. Opsin genes can be distinguished based on the wavelength of light to which they are most sensitive [Short wavelength Sensitive 1 (*SWS1*), Short

wavelength Sensitive 2 (*SWS2*), Rhodopsin class (*Rh1*), Rhodopsin Like (*Rh2*), and Long wavelength Sensitive (*LWS*)] (Hoffmann and Carleton 2009 and references therein). The *SWS2* and the *RH2* genes both have been duplicated early in the divergence of teleosts. *RH2* experienced a secondary duplication within cichlids. Each of these duplication events appears to have been through tandem duplication. As a result, cichlids possess eight functional opsin genes (*SWS1*, *SWS2A*, *SWS2B*, *Rh1*, *Rh2Aa*, *Rh2Ab*, *Rh2B*, and *LWS*), though, generally, only three cone opsins and a rod opsin are expressed at any given time. The cichlid visual system can, therefore, be tuned through the selective gene expression of these opsin genes to match their spectral environment (Hoffmann and Carleton 2009). The system can be further tuned through the segregation of alleles at these loci for minor changes in wavelength sensitivity (Seehausen et al. 2008). The divergence of opsin genes and alleles is thought to have provided cichlids with the raw material necessary for divergence through sensory drive to occur (Seehausen et al. 2008). The role that gene duplication plays in species divergence is beginning to appear as a more general phenomenon not limited to cichlids (Horth 2007).

#### 18.3.4.4 Linkage Disequilibrium

Theoretical and empirical work has examined the role that linkage, both genetic and physical, can play in the rapid phenotypic evolution and speciation (Hawthorne and Via 2001; Rundle and Nosil 2005; Dobzhansky 1951; Orr 2005; Kocher 2004). Linkage disequilibrium results from the nonrandom association of alleles at separate loci. As a result, selection on one allele results in the correlative selection of linked alleles at different loci. Selection acting on one phenotype can influence the evolutionary trajectory of a seemingly independent phenotype. This pattern is of particular interest to evolutionists when one of the loci is under strong natural selection and the other loci influence mating behavior and/or reproductive isolation.

Within cichlids, Albertson et al. (2003) found that quantitative trait loci (QTL) contributing to tooth and neurocranium shape in cichlids are linked not only to each other but also appear to be linked to genes contributing to sex determination. This has led some researchers to hypothesize the existence of “speciation chromosome” in Lake Malawi’s cichlids (Streelman and Albertson 2006). More recently, Roberts et al. (2009) identified a region within the *Pax7* gene that determines pigmentation patterns in many Lake Malawi cichlids. Individuals with one allele have a “wild-type” pigmentation pattern, while individuals with the alternative allele have a disrupted pigmentation pattern referred to as orange bloched or OB. The OB pattern is believed to confer a degree of crypsis (Roberts et al. 2009). However, the OB pattern, when expressed in males, disrupts nuptial coloration potentially causing a break down in the mate recognition system. Therefore, the OB allele is believed to be under sexually antagonistic selection: it is beneficial in females but costly in males. This conflict is believed to have been reduced by the invasion of a dominant female sex determining allele with tight linkage to the OB allele. Under such a system, individuals inheriting the OB allele would most often be female.

Roberts et al. (2009) suggest that in systems with strong sexual selection, such as East African cichlids, the costs of evolving novel phenotypes which confer opposing fitness values to the different sexes can be minimized through tight linkage to sex determining loci. In this way, novel phenotypes can evolve and spread even when in sexual conflict. Yet conflicting sex-determining systems may lead to genetic incompatibilities between nascent species and further strengthen reproductive isolation in these species.

## 18.4 Biological Conservation Issues

While terrestrial ecosystems are reasonably well protected, this is not the case for most African aquatic ecosystems. If applied, conservation strategies for aquatic biota have so far been the same as for terrestrial environments, i.e., by declaring biodiversity hotspots national parks. However, it seems questionable that this strategy will work, given the strong micro-geographic structure of the species flocks and the great degree of local endemism.

The current threats are not (yet) caused by habitat destruction and pollution but by overharvesting. Local fishermen and commercial companies developed a strong interest for exploiting the three great lakes. So far, commercial fisheries focused on large or abundant non-cichlid fishes such as the endemic Nile perches or sardines in Lake Tanganyika, the introduced Nile perch in Lake Victoria, and on endemic pelagic cichlids in Lake Malawi. Near-shore fish communities were only targeted by artisanal fishermen, which – due to their unprofessional equipment – could not harm them considerably (Coulter 1991). Commercial fishing activities face increasing problems due to overfishing, and governments reacted by enacting catch regulations. Yet, these are difficult to enforce in large lakes across national borders. In addition to the regulating efforts of governmental Fisheries Departments, stocks seemed somehow self-regulated, in that the high gasoline price made inefficient catches financially impossible for the large vessels. The reduced activities of the larger companies gave the stocks at least some time to recover. However, at least in Lake Tanganyika, the fishing strategy of the large commercial companies changed recently, towards supporting a franchise system by distributing outboard engines to local fishermen, which are to be paid for in fish returns (H. Phiri, Department of Fisheries Chilanga, personal communication). The effects of this boosted activity of local fishermen on the fish communities will be seen in the near future. The transport of frozen fish to distant markets was also decentralized, in that now not only the trucks of commercial companies deliver fish to larger cities, but also small cool-houses and trucks sustain several one-man companies. Given the enormous demand, pelagic fish communities are certainly at risk.

The second change in the fishing strategy of artisanal fishermen concerns littoral cichlid fishes. Instead of using gillnets alone and leaving them in the water for several hours, a new strategy can be observed in Lake Tanganyika: snorkeling masks and gill nets are increasingly used by local fishermen. They use the same

strategy as commercial ornamental fish catchers and snorkeling fishermen can easily target large littoral fish species on rocky and muddy substrates. Instead of placing the net in the water to specifically catch fish of the size class fitting the mesh size, divers strategically place the gill nets to actively chase in all large individuals. Near villages large specimens almost disappeared (Toby Veall, personal communication).

A recent essay suggested a novel strategy for protecting African Lake communities that accounts for their patchy distribution and local endemism (Sturmbauer 2008). The concept is analogous to the source and sink metapopulation model (Hanski and Simberloff 1997) whereby some subpopulations are being steadily harvested (sinks) and others serve as stabilizing sources (Dias 1996; Weiss 2005). The suggested strategy was derived from recent molecular phylogenetic and phylogeographic studies on East African cichlid fishes and fisheries data. It noted the following peculiarities of the endemic communities in the East African Great Lakes: While connectivity is the major problem for species in terrestrial and marine national parks (Soule 1980; Franklin 1980; Ryder 1986; Moritz 1994), to ensure a large enough effective population size of the protected animals, this is not the case in most taxa of African rivers and lakes, where microgeographic endemism prevails. Unlike many other organisms, cichlid fishes are poor dispersers. For example, most littoral cichlid species are subdivided into numerous distinct “color morphs” with restricted distribution (Sturmbauer and Meyer 1992; Verheyen et al. 1996; Rüber et al. 1999); small offspring numbers further contribute to the problem.

Sturmbauer (2008) argued that the establishment of “microscale protected areas,” a large number of small stretches of strictly protected coast line, each only some hundreds of meters long, is likely to work best to preserve the littoral cichlid communities in African lakes. Such protected zones can sustain a reasonably effective population size of littoral species, serve as spawning ground or nursery areas for pelagic species, and at the same time reseed all neighboring populations that are exploited continuously. A similar conservation strategy was recently suggested for Indo-Pacific grouper species, and the establishment of small “no-take-areas” increased the population of most grouper species by 30% over 5 years of protected status (Unsworth et al. 2007). The study on groupers also showed that a stretch of 500 m of protected area was enough to increase the population of top predatory fish. As long-term stability of littoral fishing grounds is in the immediate interest of village communities, such small protected areas should be managed and controlled by the local communities themselves, while supervised by governmental institutions.

Species diversity is not only threatened by anthropogenic causes but also by evolutionary factors. Gavrilets and Losos (2009) propose that species numbers in Lakes Victoria and Malawi will generally decline and become more similar to those observed in Tanganyika through evolutionary mechanisms. Repeated cycling of allopatric divergence and secondary admixis of the diverged species, termed species pump by Rossiter (1995), will have the following effects on species communities: Secondary admixis events will place ecologically equivalent sister species in sympatry and direct competition. Such competitive interactions might

often drive one competitor to extinction, while the distribution ranges of successful species will progressively increase (Sturmbauer 1998). In this way, species communities will be slowly homogenized along larger shore sections, and overall species numbers are likely to decrease. This scenario would explain the relatively small estimated total number of 250 endemic cichlid species in Lake Tanganyika, compared with the 500+ species of the much younger Lake Victoria and the 500–700 species of Lake Malawi with its intermediate age.

## References

- Albertson RC, Kocher TD (2005) Genetic architecture sets limits on transgressive segregation in hybrid cichlid fishes. *Evolution* 59(3):686–690
- Albertson RC, Kocher TD (2006) Genetic and developmental basis of cichlid trophic diversity. *Heredity* 97:211–221
- Albertson RC, Markert JA, Danley PD, Kocher TD (1999) Phylogeny of a rapidly evolving clade: the cichlid fishes of Lake Malawi, East Africa. *Proc Natl Acad Sci USA* 96:5107–5110
- Albertson RC, Streelman JT, Kocher TD (2003) Directional selection has shaped the oral jaws of Lake Malawi cichlid fishes. *Proc Natl Acad Sci USA* 100:5252–5257
- Almeida OG, Miranda A, Frade P, Hubbard PC, Barata EN, Canário AVM (2005) Urine as a social signal in the Mozambique Tilapia (*Oreochromis mossambicus*). *Chem Senses* 30(Suppl 1):1309–1310
- Amorim MCP (2006) Diversity of sound production in fish. In: Ladich F, Collin SP, Moller P, Kapoor BG (eds) *Communication in fishes*, vol 1. Science, Enfield, pp 71–104
- Amorim MCP, Almada VC (2005) The outcome of male-male encounters affects subsequent sound production during courtship in the cichlid fish *Oreochromis mossambicus*. *Anim Behav* 69:595–601
- Amorim MCP, Fonseca PJ, Almada VC (2003) Sound production during courtship and spawning of *Oreochromis mossambicus*: male-female and male-male interactions. *J Fish Biol* 62:658–672
- Amorim MCP, Knight ME, Stratoudakis Y, Turner GF (2004) Differences in sounds made by courting males of three closely related Lake Malawi cichlid species. *J Fish Biol* 65:1358–1371
- Amorim MCP, Simões JM, Fonseca PJ, Turner GF (2008) Species differences in courtship acoustic signals among five Lake Malawi cichlid species (*Pseudotropheus* spp.). *J Fish Biol* 72:1355–1368
- Arnegard ME, Markert JA, Danley PD, Stauffer JR, Ambali AJ, Kocher TD (1999) Population structure and colour variation of the cichlid fish *Labeotropheus fuelleborni* Ahl along a recently formed archipelago of rocky habitat patches in southern Lake Malawi. *Proc R Soc B Biol* 266:119–130
- Baldauf SA, Kullmann H, Schroth SH, Thünken T, Bakker TCM (2009) You can't always get what you want: size assortative mating by mutual mate choice as a resolution of sexual conflict. *BMC Evol Biol* 9:129
- Barata EN, Hubbard PC, Almeida OG, Miranda A, Canário AVM (2007) Male urine signals rank in the Mozambique tilapia (*Oreochromis mossambicus*). *BMC Biol* 5:54
- Barata EN, Fine JM, Hubbard PC, Almeida OG, Frade P, Sorensen PW, Canário AVM (2008) A sterol-like odorant in the urine of Mozambique tilapia males likely signals social dominance to females. *J Chem Ecol* 34:438–449
- Barlow G (2000) Cichlid fishes. Nature's grand experiment in evolution. Perseus, Cambridge, MA
- Barluenga M, Meyer A (2004) The Midas cichlid species complex: incipient sympatric speciation in Nicaraguan cichlid fishes? *Mol Ecol* 13:2061–2076

- Barluenga M, Stolting KN, Salzburger W, Muschick M, Meyer A (2006) Sympatric speciation in Nicaraguan crater lake cichlid fish. *Nature* 439:719–723
- Bell MA, Travis MP (2005) Hybridization, transgressive segregation, genetic covariation, and adaptive radiation. *Trends Ecol Evol* 20(7):358–361
- Blais J, Plenderleith M, Rico C, Taylor MI, Seehausen O, van Oosterhout C, Turner G (2009) Assortative mating among Lake Malawi cichlid fish populations is not simply predictable from male nuptial colour. *BMC Evol Biol* 9:1–12
- Boulenger GA (1898) Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History), vol 3. British Museum (Natural History), London
- Braasch I, Salzburger W, Meyer A (2006) Asymmetric evolution in two fish specifically duplicated receptor tyrosine kinase paralogs involved in teleost coloration. *Mol Biol Evol* 23:1192–1202
- Brandstätter A, Salzburger W, Sturmbauer C (2005) Mitochondrial phylogeny of the Cyprichromini, a lineage of open-water cichlid fishes endemic to Lake Tanganyika, East Africa. *Mol Phylogenet Evol* 34:382–391
- Brooks JL (1950) Speciation in ancient lakes. *Quart Rev Biol* 25:30–60
- Bruintjes R, Taborsky M (2008) Helpers in a cooperative breeder pay a high price to stay: effects of demand, helper size and sex. *Anim Behav* 75:1843–1850
- Chakrabarty P (2004) Cichlid biogeography: comment and review. *Fish Fish* 5:97–119
- Chakrabarty P (2005) Testing conjectures about morphological diversity in cichlids of Lakes Malawi and Tanganyika. *Copeia* 2005:359–373
- Clabaut C, Salzburger W, Meyer A (2005) Comparative phylogenetic analyses of the adaptive radiation of Lake Tanganyikan cichlid fish: nuclear sequences are less homoplasious but also less informative than mitochondrial DNA. *J Mol Evol* 61:666–681
- Clabaut C, Bunje PM, Salzburger W, Meyer A (2007) Geometric morphometric analyses provide evidence for the adaptive character of the Tanganyikan cichlid fish radiations. *Evol Int Org J Evol* 61:560–578
- Cohen AS, Soreghan MJ, Scholz CA (1993) Estimating the age of ancient lakes: an example from Lake Tanganyika, East African rift system. *Geology* 21:511–514
- Cohen AS, Lezzar KE, Tiercelin JJ, Soreghan M (1997) New paleo-geographic and lake-level reconstructions of Lake Tanganyika: implications for tectonic, climatic and biological evolution in a rift lake. *Basin Res* 7:107–132
- Cole TB, Stacey NE (2006) Olfactory responses to steroids in an African mouth-brooding cichlid, *Haplochromis burtoni*, (Günther). *J Fish Biol* 68:661–680
- Couldridge VCK, Alexander GJ (2002) Color patterns and species recognition in four closely related species of Lake Malawi cichlid. *Behav Ecol* 18:59–64
- Coulter GW (1991) Lake Tanganyika and its life. Oxford University Press, Oxford
- Danley PD, Husemann M, Chetta J (unpublished) Acoustic diversity in Lake Malawi's rock-dwelling cichlids
- Danley PD, Kocher TD (2001) Speciation in rapidly diverging systems: lessons from Lake Malawi. *Mol Ecol* 10:1075–1086
- Danley PD, Markert JA, Arnegard ME, Kocher TD (2000) Divergence with gene flow in the rock-dwelling cichlids of Lake Malawi. *Evolution* 54:1725–1737
- Delvaux D (1995) Age of Lake Malawi (Nyasa) and water level fluctuations. *Mus R Afr Centr Tervuren Belg Dept Geol Min Rapp Ann* 1995–1996:99–108
- Dias PC (1996) Sources and sinks in population biology. *Trends Ecol Evol* 11:326–330
- Dobzhansky TH (1951) Genetics and the origin of species, 3rd edn. Columbia University Press, New York
- Dominey WJ (1984) Effects of sexual selection and life history on speciation: species flocks in African cichlids and Hawaiian *Drosophila*. In: Echelle AA, Kornfield I (eds) Evolution of fish species flocks. University of Maine at Orono Press, Orono, ME, pp 231–250

- Duftner N, Koblmüller S, Sturmbauer C (2005) Evolutionary relationships of the Limnochromini, a tribe of benthic deep water cichlid fishes endemic to Lake Tanganyika, East Africa. *J Mol Evol* 60:277–289
- Duftner N, Sefc KM, Koblmüller S, Nevado B, Verheyen E, Phiris H, Sturmbauer C (2006) Distinct population structure in a phenotypically homogeneous rock-dwelling cichlid fish from Lake Tanganyika. *Mol Ecol* 15:2381–2395
- Eccles D, Trewavas E (1989) Malawian cichlid fishes. A classification of some haplochromine genera. Lake Fish Movies, Herten, Germany
- Farias IP, Orti G, Sampaio I, Schneider H, Meyer A (1999) Mitochondrial DNA phylogeny of the family Cichlidae: monophyly and fast molecular evolution of the Neotropical assemblage. *J Mol Evol* 48:703–711
- Farias IP, Orti G, Meyer A (2000) Total evidence: molecules, morphology, and the phylogenetics of cichlid fishes. *J Exp Zool* 288:76–92
- Frade P, Hubbard PC, Barata EN, Canário AVM (2002) Olfactory sensitivity of the Mozambique tilapia to conspecific odours. *J Fish Biol* 61:1239–1254
- Franklin IR (1980) Evolutionary change in small populations. In: Soule ME, Wilcox BA (eds) *Conservation biology: an evolutionary-ecological perspective*. Sinauer Associates, Sunderland, MA, pp 135–139
- Fryer G (2004) Speciation rates in lakes and the enigma of Lake Victoria. *Hydrobiologia* 519:167–183
- Fryer G, Iles TD (1972) The cichlid fishes of the Great Lakes of Africa: their biology and evolution. Oliver & Boyd, Edinburgh, UK
- Galis F, Metz JAJ (1998) Why are there so many cichlid species? *Trends Ecol Evol* 13:2–3
- Gasse F, Ledee V, Massault M, Fontes J-C (1989) Water-level fluctuations of Lake Tanganyika in phase with oceanic changes during the last glaciation and deglaciation. *Nature* 342:57–59
- Gavrilets S, Losos JB (2009) Adaptive radiation: contrasting theory with data. *Science* 323(5915):732–737
- Genner MJ, Seehausen O, Lunt DH, Joyce DA, Shaw PW, Carvalho GR, Turner GF (2007) Age of cichlids: new dates for ancient lake fish radiations. *Mol Biol Evol* 24:1269–1282
- Genner MJ, Knight ME, Haesler MP, Turner G (2010) Establishment and expansion of Lake Malawi rock fish populations after a dramatic Late Pleistocene lake level rise. *Mol Ecol* 19:170–182
- Giaquinto PC, Volpato GL (1997) Chemical communication, aggression, and conspecific recognition in the fish Nile Tilapia. *Physiol Behav* 62:1333–1338
- Gonzales-Voyer A, Winberg S, Kolm N (2009) Social fishes and single mothers: brain evolution in African cichlids. *Proc Roy Soc B* 276(1654):161–167
- Goodwin NB, Balshine-Earn S, Reynolds JD (1998) Evolutionary transitions in parental care in cichlid fish. *Proc R Soc B Biol Sci* 265:2265–2272
- Greenwood PH (1965) The cichlid fishes of Lake Nabugabo, Uganda. *Bull Br Mus Nat Hist Zool* 12:315–357
- Greenwood PH (1973) Morphology, endemism and speciation in African cichlid fishes. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 66:115–124
- Greenwood PH (1974) The cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. *Bull Br Mus Nat Hist Zool* 6(suppl):1–134
- Greenwood PH (1984a) What is a species flock? In: Echelle AA, Kornfield I (eds) *Evolution of fish species flocks*. University of Maine at Orono Press, Orono, Maine, pp 13–19
- Greenwood PH (1984b) African cichlids and evolutionary theories. In: Echelle AA, Kornfield I (eds) *Evolution of fish species flocks*. University of Maine at Orono Press, Orono, Maine, pp 141–155
- Hanski I, Simberloff D (1997) The metapopulation approach, its history, conceptual domain and application to conservation. In: Hanski I, Gilpin ME (eds) *Metapopulation biology: ecology, genetics and evolution*. Academic, London, pp 5–26

- Hawthorne DJ, Via S (2001) Genetic linkage of ecological specialization and reproductive isolation in pea aphids. *Nature* 412:904–907
- Herler J, Kerschbaumer M, Mitteroecker P, Postl L, Sturmbauer C (2010) Sexual dimorphism and population divergence in the Lake Tanganyika cichlid fish genus *Tropheus*. *Front Zool* 7:4
- Hoffmann CM, Carleton KL (2009) Gene duplication and differential gene expression play an important role in the diversification of visual pigments. *Integr Comp Biol* 49(6):630–643
- Horth L (2007) Sensory genes and mate choice: evidence that duplications, mutations, and adaptive evolution alter variation in mating cue genes and their receptors. *Genomics* 90:159–175
- Johnson TC, Ng'ang'a P (1990) Reflections on a rift lake. In: Katz BJ (ed) Lacustrine basin exploration: Case studies and modern analogs, American Association of Petroleum Geologists Memoir 50, pp 113–135
- Johnson TC, Scholz CA, Talbot MR, Kelts K, Ricketts RD, Ngobi G, Beuning K, Ssemamanda I, McGill JW (1996) Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science* 273:1091–1093
- Jordan R, Kellogg K, Juanes F, Stauffer J (2003) Evaluation of female mate choice cues in a group of Lake Malawi mbuna (Cichlidae). *Copeia* 2003:181–186
- Joyce DA, Lunt DH, Bill R, Turner GF, Katongo C, Duftner N, Sturmbauer C, Seehausen O (2005) An extant cichlid fish radiation emerged in an extinct Pleistocene lake. *Nature* 435:90–95
- Katongo C, Koblmüller S, Duftner N, Makasa L, Sturmbauer C (2005) Phylogeography and speciation in the *Pseudocrenilabrus philander* species complex in Zambian rivers. *Hydrobiologia* 542:221–233
- Katongo C, Koblmüller S, Duftner N, Mumba L, Sturmbauer C (2007) Evolutionary history and biogeographic affinities of the serranochromine cichlids in Zambian rivers. *Mol Phylogenet Evol* 45:326–338
- Kidd MR, Kidd CE, Kocher TD (2006) Axes of differentiation in the bower-building cichlids of Lake Malawi. *Mol Ecol* 15:459–478
- Kihlslinger RL, Klimley AP (2002) Species identity and the temporal characteristics of fish acoustic signals. *J Comp Psychol* 116:210–214
- Klett V, Meyer A (2002) What, if anything, is a tilapia? Mitochondrial ND2 phylogeny of tilapiines and the evolution of parental care systems in the African cichlid fishes. *Mol Biol Evol* 19:865–883
- Knight ME, Turner GF (1999) Reproductive isolation among closely related Lake Malawi cichlids: can males recognize conspecific females by visual cues? *Anim Behav* 58:761–768
- Knight ME, Turner GF, Rico C, van Oppen MJ, Hewitt GM (1998) Microsatellite paternity analysis on captive Lake Malawi cichlids supports reproductive isolation by direct mate choice. *Mol Ecol* 7:1605–1610
- Koblmüller S, Salzburger W, Sturmbauer C (2004) Evolutionary relationships in the sand-dwelling cichlid lineage of Lake Tanganyika suggest multiple colonization of rocky habitats and convergent origin of biparental mouthbrooding. *J Mol Evol* 58:79–96
- Koblmüller S, Duftner N, Katongo C, Phiri H, Sturmbauer C (2005) Ancient divergence in bathypelagic Lake Tanganyika deepwater cichlids: mitochondrial phylogeny of the Bathybatini. *J Mol Evol* 60:297–314
- Koblmüller S, Egger B, Sturmbauer C, Sefc KM (2007a) Evolutionary history of Lake Tanganyika's scale-eating cichlid fishes. *Mol Phylogenet Evol* 44:1295–1305
- Koblmüller S, Duftner N, Sefc KM, Aibara M, Stipacek M, Blanc M, Egger B, Sturmbauer C (2007b) Reticulate phylogeny of gastropod-shell-breeding cichlids from Lake Tanganyika: the result of repeated introgressive hybridization. *BMC Evol Biol* 7:7
- Koblmüller S, Sefc KM, Duftner N, Warum M, Sturmbauer C (2007c) Genetic population structure as indirect measure of dispersal ability in a Lake Tanganyika cichlid. *Genetica* 130:121–131



- Koblmüller S, Sefc KM, Duftner N, Katongo C, Tomljanovic T, Sturmbauer C (2008a) A single mitochondrial haplotype and nuclear genetic differentiation in sympatric colour morphs of a riverine cichlid fish. *J Evol Biol* 21:362–367
- Koblmüller S, Sefc KM, Sturmbauer C (2008b) The Lake Tanganyika cichlid species assemblage: recent advances in molecular phylogenetics. *Hydrobiologia* 615:5–20
- Koch M, Hadfield J, Sefc KM, Sturmbauer C (2008) Pedigree reconstruction in wild cichlid fish populations. *Mol Ecol* 17:4500
- Kocher TD (2004) Adaptive evolution and explosive speciation: the cichlid fish model. *Nat Rev Genet* 5:288–298
- Kornfield I (1978) Evidence for rapid speciation in Africa cichlid fishes. *Experientia* 34:335–336
- Kornfield I, Smith PF (2000) African cichlid fishes: model systems for evolutionary biology. *Annu Rev Ecol Syst* 31:163–196
- Kosswig C (1947) Selective mating as a factor for speciation in cichlid fish of East African lakes. *Nature* 159:604–605
- Kullander SO (1998) A phylogeny and classification of the South American Cichlidae (Teleostei: Perciformes). In: Malabarba L et al (eds) *Phylogeny and classification of neotropical fishes*. Edipucrs, Porto Alegre, pp 461–498
- Lezzar KE, Tiercelin JJ, De Batist M, Cohen AS, Bandora R, Bandora R, van Rensbergen C, Le Turdu C, Mifundu W, Klerx J (1996) New seismic stratigraphy and Late Tertiary history of the North Tanganyika basin, East African rift system deduced from multichannel and high-piston core evidence. *Basin Res* 8:1–28
- Liem KF (1973) Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Syst Zool* 22:425–441
- Liem KF (1991) Functional morphology. In: Keenleyside MHA (ed) *Cichlid fishes: behaviour, ecology, and evolution*. Chapman and Hall, New York, pp 129–150
- Lobel PS (1992) Sounds produced by spawning fishes. *Environ Biol Fish* 33:351–358
- Lobel PS (1998) Possible species specific courtship sounds by two sympatric cichlid fishes in Lake Malawi, Africa. *Environ Biol Fish* 52:443–452
- Loh Y-HE, Katz LS, Mims MC, Kocher TD, Yi S, Streekmann JT (2008) Comparative analysis reveals signatures of differentiation amid genomic polymorphism in Lake Malawi cichlids. *Genome Biol* 9:R1113
- Longie N, Fine ML, Parmentier E (2008) Innate sound production in the cichlid *Oreochromis niloticus*. *J Zool* 275:413–417
- Maan ME, Seehausen O, Söderberg L, Johnson L, Ripmeester EAP, Mrosso HDJ, Taylor MI, van Dooren TJM, van Alphen JJM (2004) Intraspecific sexual selection on a speciation trait, male coloration, in the Lake Victoria cichlid *Pundamilia nyererei*. *Proc R Soc Lond B* 271:2445–2452
- Maan ME, Seehausen O, Van Alphen JJM (2010) Female preferences and male coloration covary with water transparency in a Lake Victoria cichlid fish. *Biol J Linn Soc* 99:398–406
- Mabuchi K, Miya M, Azuma Y, Nishida M (2007) Independent evolution of the specialized pharyngeal jaw apparatus in cichlid and labrid fishes. *BMC Evol Biol* 7:10
- Markert JA, Arnegard ME (2007) Size dependent use of territorial space by a rock-dwelling cichlid fish. *Oecologia* 154(3):611–621
- Markert JA, Arnegard ME, Danley PD, Kocher TD (1999) Biogeography and population genetics of the Lake Malawi cichlid *Melanochromis auratus*: habitat transience, philopatry and speciation. *Mol Ecol* 8:1013–1026
- Martens K, Coulter G, Goddeeris B (1994) Speciation in ancient lakes: 40 years after Brooks. In: Martens K, Goddeeris B, Coulter G (eds) *Speciation in Ancient Lakes*. Archiv für Hydrobiologie 44: 75–96
- Mayr E (1942) *Systematics and the origin of species*. Columbia University Press, New York, USA
- Mayr E (1947) Ecological factors in speciation. *Evolution* 1:263–288
- Mayr E (1984) Evolution of fish species flocks: a commentary. In: Echelle AA, Kornfield I (eds) *Evolution of fish species flocks*. University of Maine at Orono Press, Orono, Maine, pp 3–12

- McKaye KR (1991) Sexual selection and the evolution of the cichlid fishes of Lake Malawi, Africa. In: Keenleyside MHA (ed) *Cichlid fishes: Behavior, Ecology and Evolution*. Chapman and Hall, London, pp 241–257
- McKaye KR, Louda SM, Stauffer JR (1990) Bower size and male reproductive success in a cichlid fish lek. *Am Nat* 135:597–613
- McKaye KR, Howard JH, Stauffer JR, Morgan RP II, Shonhiwa F (1993) Sexual selection and genetic relationships of a sibling species complex of bower building cichlids in Lake Malawi, Africa. *Jpn J Ichthyl* 40:15–21
- McKinnon JS, Mori S, Blackman BK, David L, Kingsley DM, Jamieson L, Chou J, Schluter D (2004) Evidence for ecology's role in speciation. *Nature* 429:294–298
- Meyer A (1993) Phylogenetic relationships and evolutionary processes in East African cichlids. *Trends Ecol Evol* 8:279–284
- Meyer A, Kocher TD, Basasibwaki P, Wilson AC (1990) Monophyletic origin of lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. *Nature* 347:550–553
- Moran P, Kornfield I (1993) Retention of an ancestral polymorphism in the Mbuna species flock (Teleostei: Cichlidae) of Lake Malawi. *Mol Biol Evol* 10:1015–1029
- Moran P, Kornfield I, Reinthal PN (1994) Molecular systematics and radiation of the haplochromine cichlids (Teleostei, Perciformes) of Lake Malawi. *Copeia* 1994:274–288
- Moritz C (1994) Defining “Evolutionary Significant Units” for conservation. *Trends Ecol Evol* 9:373–375
- Nagl S, Tichy H, Mayer WE, Takezaki N, Takahata N, Klein J (2000) The origin and age of haplochromine fishes in Lake Victoria, east Africa. *Proc R Soc B Biol Sci* 267:1049–1061
- Nelissen MHJ (1978) Sound production by some Tanganyikan cichlid fishes and a hypothesis for the evolution of their communication mechanisms. *Behaviour* 64:137–147
- Nishida M (1991) Lake Tanganyika as an evolutionary reservoir of old lineages of East African cichlid fishes: inferences from allozyme data. *Experientia* 47:974–979
- Nosil P, Harmon LJ (2009) Niche dimensionality and ecological speciation. In: Butlin R, Bridle J, Schluter D (eds) *Speciation and patterns of diversity*. Cambridge University Press, Cambridge, pp 127–154
- Odhiambo E, Kerschbaumer E, Postl L, Sturmbauer C (2011) Morphometric differentiation among haplochromine cichlid fish species of a satellite lake of Lake Victoria. *J Zool Syst Evol Res* 49, doi:10.1111/j.1439-0469.2011.00624.x
- Ohno S (1970) *Evolution by Gene Duplication*. Springer, New York
- Orr HA (2005) The genetic theory of adaptation: a brief history. *Nat Rev Gen* 6:119–127
- Owen RB, Crossley R, Johnson TC, Tweddle D, Kornfield I, Davison S, Eccles DH, Endstrom DE (1990) Major low levels of Lake Malawi and their implications for speciation rates in cichlid fishes. *Proc Roy Soc Lond B* 240:519–553
- Parnell NF, Hulsey CD, Streebman JT (2008) Hybridization produces novelty when the mapping of form to function is many to one. *BMC Evol Biol* 8:122
- Phillips CT, Johnston CE (2008) Geographical divergence of acoustic signals in *Cyprinella galactura*, the whitetail shiner (Cyprinidae). *Anim Behav* 75:617–626
- Pierotti MER, Knight ME, Immler S, Barson NJ, Turner GF, Seehausen O (2008) Individual variation in male mating preferences for female coloration in a polymorphic cichlid fish. *Behav Ecol* 19:483–488
- Plenderleith M, van Oosterhout C, Robinson RL, Turner GF (2005) Female preference for conspecific males based on olfactory cues in a Lake Malawi cichlid fish. *Biol Lett* 1:411–414
- Rensch B (1933) *Zoologische Systematik und Artbildungsproblem*. Verhandlungen der deutschen Zoologischen Gesellschaft 1933:19–83
- Ribbink AJ, Marsh BA, Marsh AC, Ribbink AC, Sharp BJ (1983) A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. *S Afr J Zool* 18:148–310
- Rico C, Turner GF (2002) Extreme microallopatric divergence in a cichlid species from Lake Malawi. *Mol Ecol* 11:1585–1590
- Rieseberg LH (1999) Transgressive segregation, adaptation, and speciation. *Heredity* 83:363–372

- Ripley JL, Lobel PS (2004) Correlation of acoustic and visual signals in the cichlid fish, *Tramitichromis intermedius*. *Environ Biol Fish* 71:389–394
- Roberts RB, Ser JR, Kocher TD (2009) Sexual conflict resolved by the invasion of a novel sex determiner in Lake Malawi cichlid fishes. *Science* 326(5955):989–1001
- Robinson RR, Fernald RD, Stacey NE (1998) The olfactory system of a cichlid fish responds to steroidal compounds. *J Fish Biol* 53:226–229
- Rossiter A (1995) The cichlid fish assemblage of Lake Tanganyika: Ecology, behavior and evolution of its species flock. *Adv Ecol Res* 26:157–252
- Rossiter A, Yamagishi S (1997) Intraspecific plasticity in the social system and mating behaviour of a lek-breeding cichlid fish. In: Kawanabe H, Hori M, Nagoshi M (eds) *Fish communities in Lake Tanganyika*. Kyoto University Press, Kyoto, Japan, pp 293–318
- Rüber L, Verheyen E, Meyer A (1999) Replicated evolution of trophic specializations in an endemic cichlid fish lineage from Lake Tanganyika. *Proc Natl Acad Sci USA* 96:10230–10235
- Rüber L, Meyer A, Strumbauer C, Verheyen E (2001) Population structure in two sympatric species of the Lake Tanganyika cichlid tribe Eretmodini: evidence for introgression. *Mol Ecol* 10:1207–1225
- Rundle HD, Nosil P (2005) Ecological Speciation. *Ecol Lett* 8(3):336–352
- Ryder OA (1986) Species conservation and systematics: the dilemma of subspecies. *Trends Ecol Evol* 1:9–10
- Salzburger W (2009) The interaction of sexually and naturally selected traits in the adaptive radiations of cichlid fishes. *Mol Ecol* 18:169–185
- Salzburger W, Meyer A (2004) The species flocks of East African cichlid fishes: recent advances in molecular phylogenetics and population genetics. *Naturwissenschaften* 91:277–290
- Salzburger W, Baric S, Sturmbauer C (2002a) Speciation via introgressive hybridization in East African cichlids? *Mol Ecol* 11:619–625
- Salzburger W, Meyer A, Baric S, Verheyen E, Sturmbauer C (2002b) Phylogeny of the Lake Tanganyika cichlid species flock and its relationship to the Central and East African haplochromine cichlid fish faunas. *Syst Biol* 51:113–135
- Salzburger W, Mack T, Verheyen E, Meyer A (2005) Out of Tanganyika: Genesis, explosive speciation, key-innovations and phylogeography of the haplochromine cichlid fishes. *BMC Evol Biol* 5:17
- Schliwen UK, Klee B (2004) Reticulate speciation in Cameroonian crater lake cichlids. *Front Zool* 1:5
- Schliwen UK, Tautz D, Pääbo S (1994) Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* 368:629–632
- Schliwen U, Rassman K, Markmann M, Markert J, Kocher T, Tautz D (2001) Genetic and ecological divergence of a monophyletic cichlid species pair under fully sympatric conditions in Lake Ejagham, Cameroon. *Mol Ecol* 10:1471–1488
- Schluter D (1996) Ecological causes of adaptive radiation. *Am Nat* 148(Suppl):S40–S64
- Schluter D (2000) *The ecology of adaptive radiation*. Oxford University Press, Oxford
- Schluter D, McPhail JD (1993) Character displacement and replicate adaptive radiation. *Trends Ecol Evol* 8:197–200
- Scholz CA, Rosendahl B (1988) Low lake stands in Lakes Malawi and Tanganyika, delineated with multifold seismic data. *Science* 277:1645–1648
- Scholz CA, King JW, Ellis GS, Swart PK, Stager JC, Colman SM (2003) Palaeolimnology of Lake Tanganyika, East Africa, over the past 100 k yr. *J Palaolimnology* 30:139–150
- Scholz CA, Johnson TC, Cohen AS, King JW, Peck JA, Overpeck JT, Talbot MR, Brown ET, Kalindekafu L, Amoako PYO, Lyons RP, Shanahan TM, Castaneda IS, Heil CW, Forman SL, McHargue LR, Beuning KR, Gomez J, Pierson J (2007) East African megadroughts between 135 and 75 thousand years ago and bearing on early-modern human origins. *Proc Natl Acad Sci USA*. doi:10.1073/pnas.0703874104
- Seehausen O (2000) Explosive speciation rates and unusual species richness in haplochromine cichlid fishes: effects of sexual selection. *Adv Ecol Res* 31:237–274

- Seehausen O (2002) Patterns in cichlid fish radiation are compatible with Pleistocene desiccation of Lake Victoria and 14.600 year history for its cichlid species flock. *Proc Roy Soc Lond B* 269:491–497
- Seehausen O (2004) Hybridization and adaptive radiation. *Trends Ecol Evol* 19:198–207
- Seehausen O (2006) African cichlid fish: a model system in adaptive radiation research. *Proc R Soc B Biol Sci* 273:1987–1998
- Seehausen O, Van Alphen JJM (1998) The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex). *Behav Ecol Sociobiol* 42:1–8
- Seehausen O, van Alphen JJM (1999) Can sympatric speciation by disruptive sexual selection explain rapid evolution of cichlid diversity in Lake Victoria? *Ecol Lett* 2:262–271
- Seehausen O, van Alphen JJM, Witte F (1997) Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277:1808–1811
- Seehausen O, Koetsier E, Schneider MV, Chapman LJ, Chapman CA, Knight ME, Turner GF, van Alphen JJM, Bills R (2003) Nuclear markers reveal unexpected genetic variation and Congolese-Nilotic origin of the Lake Victoria cichlid species flock. *Proc R Soc Lond B* 270:129–137
- Seehausen O, Terai Y, Magalhaes IS, Carleton KL, Mrosso HDJ, Miyagi R, van der Sluijs I, Schneider MV, Maan ME, Tachida H, Imai H, Okada N (2008) Speciation through sensory drive in cichlid fish. *Nature* 455:620–626
- Sefc KM, Baric S, Salzburger W, Sturmbauer C (2007) Species-species population structure in rock-specialized sympatric cichlid species in Lake Tanganyika, East Africa. *J Mol Evol* 64:33–49
- Sides J, Lydeard C (2000) Phylogenetic utility of the tyrosine kinase gene X-src for assessing relationships among representative cichlid fishes. *Mol Phylogenet Evol* 14:51–74
- Simões JM, Duarte IG, Fonseca PJ, Turner GF, Amorim MCP (2006) Acoustic behaviour in Malawian cichlids (*Pseudotropheus*, Cichlidae): Potential cues for species recognition and intraspecific communication. *Razprave IV razreda SAZU* 47(3):229–236
- Simões JM, Fonseca PJ, Turner GF, Amorim MCP (2008) Courtship and agonistic sounds by the cichlid fish *Pseudotropheus zebra*. *J Acoust Soc Am* 124:1332–1339
- Smith PF, Kornfield I (2002) Phylogeography of Lake Malawi cichlid of the genus *Pseudotropheus*: significance of allopatric color variation. *Proc R Soc Lond B* 269:2495–2502
- Smith AR, van Staaden MJ (2009) The association of visual and acoustic courtship behaviors in African cichlid fishes. *Mar Freshw Behav Phy* 42:211–216
- Soule ME (1980) Thresholds for survival: maintaining fitness and evolutionary potential. In: Soule ME, Wilcox BA (eds) *Conservation Biology: an Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, MA, pp 151–169
- Sparks JS (2004) Molecular phylogeny and biogeography of the Malagasy and South Asian cichlid fishes (Teleostei: Perciformes: Cichlidae). *Mol Phylogenet Evol* 30:599–614
- Stauffer JR, McKaye KR, Konings AF (2002) Behaviour: an important diagnostic tool for Lake Malawi cichlids. *Fish* 3:213–224
- Stauffer JR, Kellogg KA, McKaye KR (2005) Experimental evidence of female choice in Lake Malawi cichlids. *Copeia* 2005(5):657–660
- Stelkens RB, Seehausen O (2009) Phenotypic divergence but not genetic distance predicts assortative mating among species of a cichlid fish radiation. *J Evol Biol* 22:1679–1694
- Stelkens RB, Pierotti ME, Joyce DA, Smith AM, Sluijs IV, Seehausen O (2008) Disruptive sexual selection on male nuptial coloration in an experimental hybrid population of cichlid fish. *Phil Trans R Soc B Biol Sci* 363:2861–2870
- Stepien CA, Kocher TD (1997) Molecules and morphology in studies of fish evolution. In: Kocher TD, Stepien CA (eds) *Molecular Systematics of Fishes*. Academic, San Diego, California, pp 1–11

- Stiassny MLJ (1991) Phylogenetic interrelationships of the family Cichlidae: an overview. In: Keenleyside MHA (ed) *Cichlid Fishes, Behaviour. Ecology and Evolution*. Chapman & Hall, London, pp 1–35
- Stiassny MLJ, Meyer A (1999) Cichlids of rifts lakes. *Sci Am* 280:64–69
- Streelman JT, Albertson RC (2006) Evolution of novelty in the cichlid dentition. *J Exp Zool B Mol Dev Evol* 306:216–226
- Streelman JT, Danley PD (2003) The stages of vertebrate evolutionary radiation. *Trends Ecol Evol* 18:126–131
- Streelman JT, Zardoya R, Meyer A, Karl SA (1998) Multilocus phylogeny of cichlid fishes (Pisces: Perciformes): Evolutionary comparisons of microsatellite and single-copy nuclear loci. *Mol Biol Evol* 15:798–808
- Streelman JT, Gmyrek SL, Kidd MR, Kidd C, Robinson RL, Hert E, Ambali AJ, Kocher TD (2004) Hybridization and contemporary evolution in an introduced cichlid fish from Lake Malawi National Park. *Mol Ecol* 13:2471–2479
- Streelman JT, Albertson RC, Kocher TD (2007) Variation in body size and trophic morphology within and among genetically differentiated populations of the cichlid fish, *Mtetracima zebra*, from Lake Malawi. *Freshw Biol* 52:525–538
- Sturmbauer C (1998) Explosive speciation in cichlid fishes of the African Great Lakes: a dynamic model of adaptive radiation. *J Fish Biol* 53(Suppl A):18–36
- Sturmbauer C (2008) The Great Lakes in East Africa: biological conservation considerations for species flocks. *Hydrobiologia* 615:95–101
- Sturmbauer C, Meyer A (1992) Genetic divergence, speciation and morphological stasis in a lineage of African cichlid fishes. *Nature* 358:578–581
- Sturmbauer C, Meyer A (1993) Mitochondrial phylogeny of the endemic mouthbrooding lineages of cichlid fishes of Lake Tanganyika, East Africa. *Mol Biol Evol* 10:751–768
- Sturmbauer C, Baric S, Salzburger W, Rüber L, Verheyen E (2001) Lake level fluctuations synchronize genetic divergences of cichlid fishes in African lakes. *Mol Biol Evol* 18:144–154
- Sturmbauer C, Hainz U, Baric S, Verheyen E, Salzburger W (2003) Evolution of the tribe Tropheini from Lake Tanganyika: synchronized explosive speciation producing multiple evolutionary parallelism. *Hydrobiologia* 500:51–64
- Sugawara T, Teari Y, Imai H, Turner GF, Koblmüller S, Sturmbauer C, Shichida Y, Okada N (2005) Parallelism of amino acid changes at the RH1 affecting spectral sensitivity among deep-water cichlids from Lakes Tanganyika and Malawi. *Proc Natl Acad Sci USA* 102:5448–5453
- Takahashi T (2003) Systematics of Tanganyikan cichlid fishes (Teleostei: Perciformes). *Ichthyol Res* 50:367–382
- Takahashi K, Okada N (2002) Mosaic structure and retropositional dynamics during evolution of subfamilies of short interspersed elements in African cichlids. *Mol Biol Evol* 19:1303–1312
- Takahashi K, Terai Y, Nishida M, Okada N (2001) Phylogenetic relationships and ancient incomplete lineage sorting among cichlid fishes in Lake Tanganyika as revealed by analysis of the insertion of retroposons. *Mol Biol Evol* 18:2057–2066
- Terai Y, Morikawa N, Kawakami K, Okada N (2003) The complexity of alternative splicing of hageromo mRNAs is increased in an explosively speciated lineage in East African cichlids. *Proc Natl Acad Sci USA* 100:12798–12803
- Tiercelin J-J, Mondeguer A (1991) The geology of the Tanganyika trough. In: Coulter GW (ed) *Lake Tanganyika and its life*. Oxford University Press, New York, pp 7–48
- Turner GF (2007) Adaptive radiation of cichlid fish. *Curr Biol* 17:R827–R831
- Turner GF, Burrows MT (1995) A model of sympatric speciation by sexual selection. *Proc R Soc B Biol Sci* 260:287–292
- Turner GF, Seehausen O, Knight ME, Allender C, Robinson RL (2001) How many species of cichlid fishes are there in African lakes? *Mol Ecol* 10:793–806
- Tweedle D, Eccles DH, Frith CB, Fryer G, Jackson PBN, Lewis DSC, Lowe-McConnell R (1998) Cichlid spawning structures – bowers or nests. *Environ Biol Fish* 51:107–109

- Unsworth RKF, Powell A, Hukom F, Smith JD (2007) The ecology of Indo-Pacific grouper (Serranidae) species and the effects of a small-scale no take area on grouper assemblage, abundance and size frequency distribution. *Mar Biol* 152:243–254
- van Oppen MJH, Turner GF, Rico C, Deutsch JC, Ibrahim KM, Robinson RL, Hewitt GM (1997) Unusually fine-scale genetic structuring found in rapidly speciating Malawi cichlid fishes. *Proc R Soc B Biol Sci* 264:1803–1812
- van Oppen MJH, Turner GF, Rico C, Robinson RL, Deutsch JC, Genner MJ, Hewitt GM (1998) Assortative mating among rock-dwelling cichlid fishes supports high estimates of species richness from Lake Malawi. *Mol Ecol* 7:991–1001
- Weesky MD, Andraso GM, Ropski SJ (2005) Behavior of male Kenyi Cichlids, *Pseudotropheus lombardoi*, in response to visual and olfactory cues from females. *Bios* 76:77–83
- Verheyen E, Rüber L, Snoeks J, Meyer A (1996) Mitochondrial phylogeography of rock dwelling cichlid fishes reveals evolutionary influence of historic lake level fluctuations in Lake Tanganyika, Africa. *Phil Trans Roy Soc Lond B* 351:797–805
- Verheyen E, Salzburger W, Snoeks J, Meyer A (2003) Origin of the superflock of cichlid fishes from Lake Victoria, East Africa. *Science* 300:325–329
- Wagner CE, McCune AR (2009) Contrasting patterns of spatial genetic structure in sympatric rock-dwelling cichlid fishes. *Evolution* 63:1312–1326
- Watanabe M, Hiraide K, Okada N (2007) Functional diversification of kir7.1 in cichlids accelerated by gene duplication. *Gene* 399:46–52
- Weiss S (2005) Keynote address: conservation genetics of freshwater organisms. *Bulletin Français de la Pêche et de la Pisciculture* 376:571–583
- Werner NY, Mokady O (2004) Swimming out of Africa: mitochondrial DNA evidence for late Pliocene dispersal of a cichlid from Central Africa to the Levant. *Biol J Lin Soc* 82:103–109
- Woltereck R (1931) Beobachtungen und Versuche zum Fragenkomplex der Artbildung. *Biologisches Centralblatt* 51:231–253
- Young KA, Genner MJ, Joyce DA, Haesler MP (2009) Hotshots, hot spots, and female preference: exploring lek formation models with a bower-building cichlid fish. *Behav Ecol* 20:609–615
- Zardoya R, Vollmer DM, Craddock C, Streelman JT, Karl S, Meyer A (1996) Evolutionary conservation of microsatellite flanking regions and their utility in resolving the phylogeny of cichlid fishes (Pisces: Perciformes). *Proc Roy Soc Lond B* 263:1611–1618