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Addis Ababa, Ethiopia, 22–26 September 2008

Jos Snoeks & Abebe Getahun (eds)
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DE L'AFRIQUE CENTRALE

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Foreword

The Fourth International Conference on African Fish and Fisheries was held in Addis Ababa, Ethiopia, from 22 to 26 September 2008.

About 230 participants from more than 30 countries, 18 of which are in Africa, attended the six plenary lectures and over 150 presentations (oral or poster). The conference was organized by the Department of Biology of the Addis Ababa University and the Ethiopian Fisheries and Aquatic Sciences Association (EFASA), and financially supported by the following sponsors: the Royal Museum for Central Africa, Tervuren, Belgium; the American Museum of Natural History, New York, USA; the Canadian International Development Agency (CIDA), Canada; the Institut de Recherche pour le Développement (IRD), France; the Joint Ethio-Russian Biological Expedition (JERBE), Ethiopia; the Sub-Regional Office for Eastern Africa of the FAO, Ethiopia; the Technical Centre for Agricultural and Rural Cooperation (CTA)*,* the Netherlands; and the Addis Ababa University, Ethiopia.

All manuscripts were submitted to at least two referees and the editors. We want to thank all referees for their kind contribution.

We thank the publications service of the Royal Museum for Central Africa for their assistance and especially Isabelle Gérard for her collaborative spirit.

This volume is dedicated to the late Frans Witte, who passed away suddenly on the 12th of February 2013 while under treatment for cancer. Frans was one of the keynote speakers of the meeting and wrote a chapter in these proceedings. Frans was a passionate, excellent scientist, who could fill his audience with enthusiasm not by using big words or exaggerating, but with well-structured lectures based on the enormous knowledge he had acquired over several decades of studying the Lake Victoria basin. Numerous key publications on this major aquatic ecosystem in a state of flux were co-authored by him. Frans also received two 'Best teacher' awards thanks to his didactic skills and determination to help students. We should not forget that above all, he was a warm, friendly and gentle person.

J. Snoeks & A. Getahun

Conservation and Management of Freshwaters in a Changing World

Robin Abell[1]

ABSTRACT

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Inland water systems and species are on average around the world more imperiled than their terrestrial and marine counterparts. With threats to freshwater systems growing, effectively conserving and managing inland water biodiversity and the ecological functions that underpin essential ecosystem services will require more than maintaining the conservation status quo. This paper reviews some new datasets and emerging strategies for conserving freshwaters around the world. Strategies discussed are protected areas, environmental flows, ecosystem services, climate change adaptation, and market transformation. Many of these strategies are undertaken principally for reasons other than conserving freshwater species and habitats, but freshwater systems, functions, and resources are central to the strategies' success and freshwater conservation targets may receive secondary benefits. None of these strategies on their own is a silver bullet for inland water systems conservation, and the efficacy of most to achieve their goals has yet to be rigorously evaluated. Undertaking more rigorous evaluations will help to clarify which strategies work and in what circumstances, and will provide exciting research opportunities for a new generation of scientists and practitioners.

Keywords: strategies; protected areas; ecosystem services; environmental flows; climate change adaptation; water footprint; evidence-based conservation

INTRODUCTION

The conservation community widely acknowledges the urgent need to conserve freshwater species and systems, and new data reinforce this mandate. The 2010 IUCN Red List of Threatened Species finds that 34% of freshwater fish species assessed are imperiled, along with 55% of assessed freshwater mollusks and 33% of the world's freshwater amphibians (IUCN 2010). A review by Strayer and Dudgeon (2010) confirms that in more developed countries, over one-third of some freshwater taxonomic groups are extinct or imperiled. WWF's Living Planet Index estimates that a subset of freshwater species populations declined by an average of 37% from 1970 to 2008, underscoring a pattern of greater decline than for either terrestrial or marine populations (WWF 2012). The same index found that tropical fish species declined by 70%. Statistics on the loss and degradation of freshwater habitats are equally grim (see, for instance, Millennium Ecosystem Assessment 2005). Despite the clear need to act, the conservation community's investment in freshwater initiatives has been relatively anemic. Budget numbers for pro-

gram expenditures are unavailable, but a survey of scientific publications by staff from the three largest international conservation organizations (WWF, The Nature Conservancy, and Conservation International) found that between January 2003 and December 2012, more than twice as many terrestrial publications were produced as those focused on freshwater systems (Web of Science, accessed 26 June 2013). During that same time period, conservation staff produced four times as many scientific publications about five flagship mammal groups (tigers, rhinos, elephants, gorillas, and whales) as about freshwater fish, the former encompassing about 100 species and the latter comprising over 13,000 species, or about a quarter of all vertebrates (Dudgeon *et al.* 2006).

It would be easy to dismiss this apparent disconnect between conservation need and investment as the result of a charisma gap. After all, most freshwater species lack the physical attributes that people find appealing (Stokes 2007). However, that explanation is perhaps too facile. A paucity of foundational information describing aquatic taxa and their habitats has created real challenges for their conservation. Research to fill these data gaps has certainly suf-

fered from insufficient resources, but there is also the reality that broad-scale mapping and assessment of dynamic freshwater systems is in many ways more complex than for terrestrial systems. Some recent advances, particularly in the use of new remote sensing data, show promise for filling some of these gaps, and recent publications like IUCN's Pan-African Freshwater Biodiversity Assessment (Darwall *et al.* 2011) are providing detailed data syntheses for the first time for certain regions.

Another possible source of optimism is that the disconnect between need and investment, while real, appears less extreme when recognizing that quite a number of conservation efforts underway have the potential to directly or indirectly benefit inland aquatic species. These efforts often lack a freshwater label, even though protecting and managing freshwater systems are central to their success.

This paper takes a forward-looking view, highlighting some of these newer datasets and strategies that may be put into the service of freshwater conservation. It ends with a discussion of how freshwater scientists and managers can contribute to making the strategies more effective. The strategies presented here are far from comprehensive but they are representative of what the leading edge in freshwater conservation – and conservation more generally – looks like today.

INFORMATION GAPS

There is broad agreement that, in general around the world, freshwater fishes and other freshwater groups are poorly studied. A number of publications have addressed this issue and note that informa-

tion on freshwater species is highly skewed toward a small number of well-studied geographies (e.g. Lundberg *et al.* 2000; Dudgeon *et al.* 2006; Regnier *et al.* 2009). Information gaps are not simply an academic issue; not knowing about biodiversity is a real impediment to protecting it. For instance, if we assume that conservation success is in part a function of conservation investment, the case of the Global Environment Facility (GEF) is illustrative. The GEF, which makes over $1 billion in environmental grants annually, adopted a new Resource Allocation Framework in 2005 to guide its investment decisions. Global data on terrestrial ecoregions and their biodiversity values were a key set of inputs to the framework, but the lack of parallel freshwater datasets at the time meant that freshwater biodiversity considerations were absent (GEF 2005; Abell *et al.* 2008).

From a conservation perspective, certain information gaps are more critical to fill than others. One fundamental type of information is geographic. Conservation is inherently spatial, but for many parts of the world, the best distribution data we have are assignments of aquatic species to broad zoogeographic regions, continents, countries, or major river basins (e.g. Balian *et al.* 2008; Leveque *et al.* 2008). That level of geographic resolution is insufficient. Without reasonably comprehensive, detailed, and accurate information describing freshwater species and habitat distributions, it can be challenging to get beyond the first step in a conservation planning process.

Efforts are underway to begin to address this gap. For instance, WWF and The Nature Conservancy, working with hundreds of international experts, developed Freshwater Ecoregions of the World (www.feow.org) The 426 ecoregions were delineated primarily based
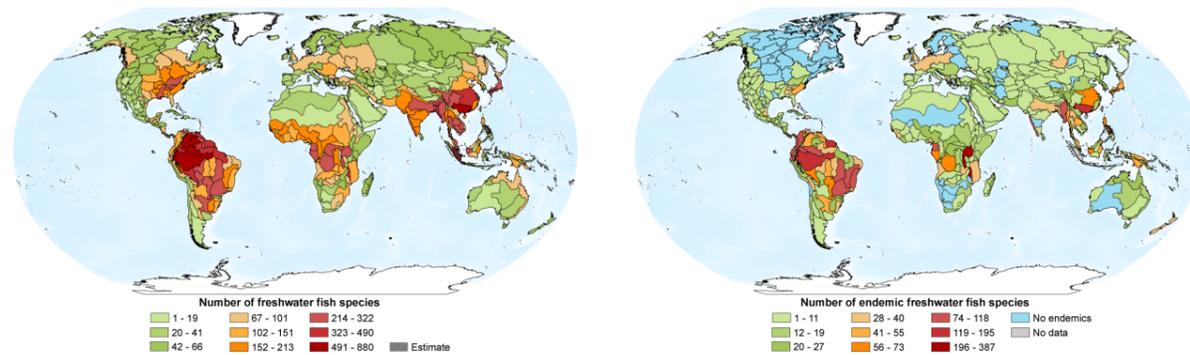
on freshwater fish zoogeography, and the project involved compiling freshwater fish species lists for all ecoregions (Abell *et al.* 2008). These lists in turn allow production of global maps of richness and endemism (Fig. 1a-b) and other analyses that can inform conservation investments globally and regionally (Abell *et al.* 2011).

Freshwater Ecoregions of the World represents a first in terms of mapping fish species data into biogeographically-meaningful units for virtually the entire non-marine surface of the earth, but finer-scale conservation planning requires finer-resolution maps. For effective conservation planning, species lists tied to fixed ecoregions or other large units have limited utility. Instead, we need species occurrences linked as precisely as possible to specific freshwater systems or small watersheds at the highest resolution possible. This level of 'hydrographic georeferencing' would allow for a whole host of conservation applications. Species lists could be generated for any user-defined watershed; species-habitat associations could be examined; species distributions could be more reliably visualized and modeled; upstream and upland threats could be evaluated; and biodiversity data could be better integrated into water resource management decisions, environmental flows assess-

ments, and other river-focused sustainable development efforts. Ultimately, an interactive global freshwater species atlas could be generated.

Until recently, the hydrographic data required for this kind of georeferencing did not exist for most parts of the world. Now, though, the data are available globally in the form of HydroSHEDS (www.hydrosheds.org) (Fig. 2) (Lehner *et al.* 2008). The dataset is based on 90-m resolution elevation data obtained during a Space Shuttle flight for NASA's Shuttle Radar Topography Mission (SRTM). In addition to permitting streams to be mapped at exceptionally high resolution, it far exceeds existing global hydrographic datasets in terms of accuracy. Widely-available tools for georeferencing freshwater species to streams and watersheds do not yet exist, but the rapid use of new hydrographic datasets like HydroSHEDS for conservation applications suggests that such tools will emerge soon (e.g. Nel *et al.* 2007). Digitally linking species occurrences to hydrographic base maps is an exciting frontier for freshwater biodiversity conservation and has the potential to leapfrog over the geospatial technologies and datasets currently in use for terrestrial systems, where species often hover in geographic space rather than sit in specific landscapes/aquascapes.

Fig. 1a-b. Freshwater fish species richness (left) and endemism (right) by freshwater ecoregion. Modified from Abell *et al.* 2008.
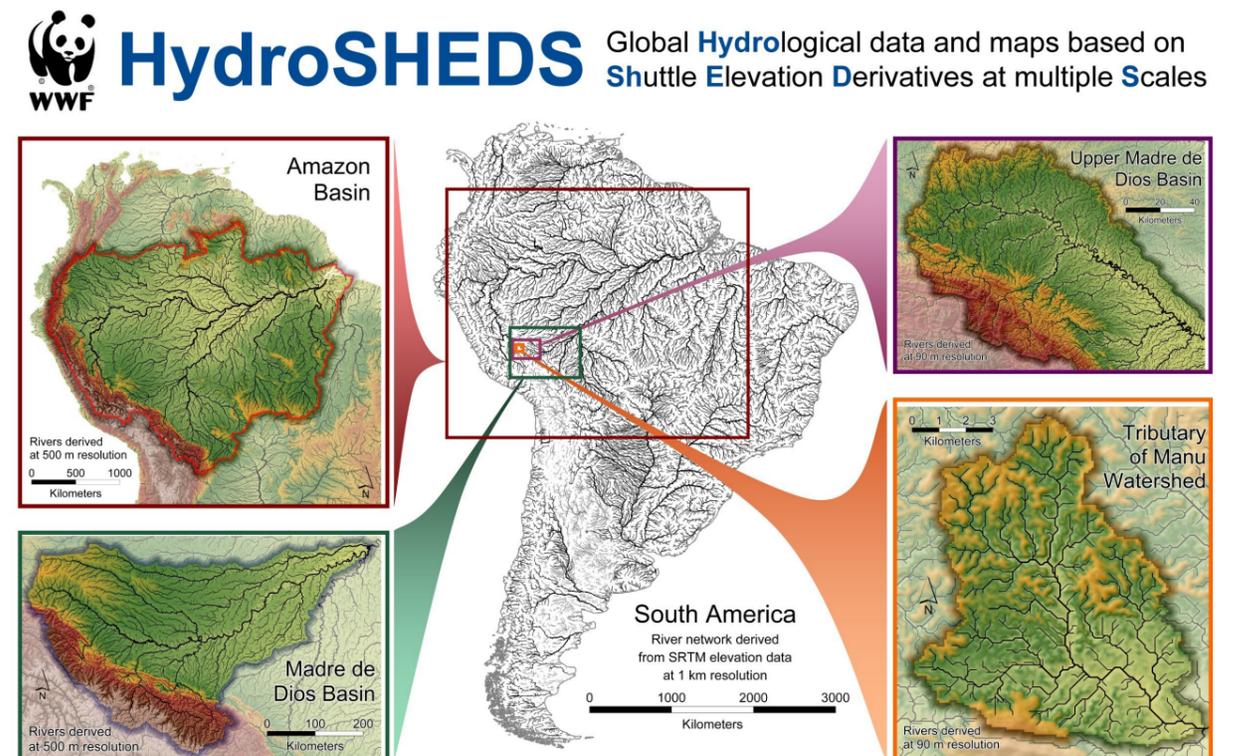
Fig. 2. Streams and drainage basins of South America's Amazon River Basin, as mapped using HydroSHEDS data.

CONSERVATION STRATEGIES

Better data describing freshwater species and habitats, and in particular describing their distributions, should facilitate the development and implementation of more effective conservation strategies. Our collective freshwater conservation toolbox contains any number of strategies, both traditional (e.g. pollution control) and more cutting-edge (e.g. payments for ecosystem services). Some are implemented locally, and others will be larger in both scale and impact (Fig. 3). Virtually all of the strategies in our toolbox are implemented in specific places, underscoring that although threats are increasingly globalized, originating sometimes in distant markets, solutions will always to some extent be local. Several strategies garnering increasing attention are detailed here.
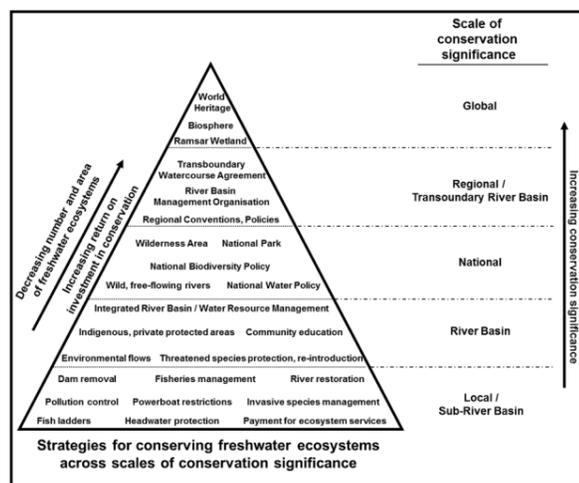
Fig. 3. Strategies for river conservation, organized in terms of geographic scale (right) and scale of impact (left). All freshwater ecosystems have conservation significance. Strategies are complementary and additive. Effectively conserving freshwater ecosystems of higher conservation significance relies upon strategies used for conserving ecosystems of lower significance. From Abell *et al.* 2009.

Protected areas

Protected areas, also called reserves, parks, preserves, and refuges, have been a cornerstone of conservation for over a century (Phillips 2004). Protected areas (PAs) may be an old conservation strategy, but research into the potential of PAs to conserve freshwaters is relatively new. We know that PAs cover about 12% of the non-marine surface of the earth, so by definition they both encompass

and drain to freshwater systems (Chape *et al.* 2003). With the exception of inland Ramsar sites, though, which are designated around wetlands, most PAs have not been designated, designed, or managed for the conservation of freshwater species and habitats. Even though we know that freshwaters must benefit at least somewhat from the PAs within which they occur, and from those PAs upstream and possibly even downstream, we have no way currently of evaluating the extent of that benefit. With new datasets like HydroSHEDS allowing more sophisticated geospatial analyses, and a recognition that we have not made the best use of PAs as a freshwater conservation tool, the intersection of freshwaters and PAs is gaining increased attention (Abell *et al.* 2007; Cucherousset *et al.* 2007; Nel *et al.* 2007; Roux *et al.* 2008; Nel *et al.* 2009; Thieme *et al.* 2012). Exploring the intersection of freshwaters and PAs can expand how the broader conservation community thinks about PAs overall. For instance, protected free-flowing rivers are in some ways a close equivalent to traditional terrestrial protected areas, in that they have been designated to maintain rivers' natural (or near-natural) states and that certain modifications, like impoundments, are typically prohibited. Currently, formal programs for protecting free-flowing rivers exist only in the U.S., Canada, and parts of Australia, but discussions about protecting rivers in their own right are spreading to other parts of the world (Anderson *et al.* 2006; Poff *et al.* 2007; Nel *et al.* 2009). If river protection programmes expand they may pose a challenge to global protected area accounting systems, as presently the World Database on Protected Areas can accommodate data describing polygonal but not linear PAs (Abell *et al.* 2007). Modification of such accounting systems could be a small first step in enlarging the larger PA paradigm to encompass rivers, whose current function is often only to demarcate PA boundaries (Peres & Terborgh 1995; Nel *et al.* 2009).

A second type of PA that challenges traditional notions is the fishery or harvest reserve, or sanctuary. These are typically designated with the goal of maintaining or enhancing fishery stocks outside the reserves (Demartini 1993). Many if not most of these areas are community-managed or co-managed and, like protected free-flowing rivers, are rarely counted within global PA inventories (Hoggarth *et al.* 1999; Bene *et al.* 2009). Importantly, these reserves can shift

in space and time to track the movements and critical life history stages of fishery species (Ruffino 2001). A conservation strategy that embraces the natural dynamism of freshwater systems and species may have broader lessons for PAs generally, especially if future climate conditions force PA management to extend beyond existing PA boundaries (Gaston et al. 2008). A final type of freshwater PA, broadly defined, is the riparian reserve or buffer. As a core conservation strategy (Osborne & Kovacic 1993), riparian buffers – managed or 'reserved' stream- or lake-side lands – are to freshwater conservation as traditional parks are to terrestrial conservation. Countries around the world have promulgated forestry and other land use codes requiring riparian buffers, though such codes are often unenforced (Moore & Bull 2004). While riparian buffers may not qualify as protected areas according to widely accepted definitions (e.g. Dudley 2008), they may be increasingly representative of a new type of climate change adaptation strategy: areas that confer resilience by buffering stress (e.g. **providing temperature regulation through streamside shade**) and supporting fundamental ecosystem processes (e.g. **contributing allochthonous organic matter**); that maintain connectivity to facilitate species migration and dispersal; and that can be applied with relatively modest expense nearly universally, including and especially outside fixed PAs (Killeen & Solorzano 2008).

These three types of freshwater PAs can be classified broadly as place-based protections. The often complementary nature of these strategies underscores that no single type of place-based protection will be sufficient in most cases, and that place-based protections for freshwaters can take many forms. Some are typical PAs, like national parks or wildlife reserves, which by nature of their land cover protection and activities restriction will in most cases provide some benefit to freshwaters. Others may not be PAs at all; protections like certified forests or aquifer recharge zones might collectively be called freshwater protection areas (Abell et al. 2007). These kinds of areas can be visualized together to illustrate the breadth of place-based strategies available to freshwater conservation planners and managers (Fig. 4). **We show them within a larger catchment** not to suggest that all strategies would occur in a single catchment but instead to emphasize the importance of understanding any given strategy within a larger catchment context.

Place-based tools for protecting freshwater ecosystems
1. National Park / Wildlife Reserve
2. Wild / Heritage River
3. Private Protected Area / Conservancy
4. Ramsar Wetland
5. Wetland protection zoning
6. Fisheries / Aquatic Reserve
7. Urban Land Use Zoning
8. Community Conserved Area
9. Water Supply Catchment
10. Aquifer Recharge Area
11. Marine Park / Reserve
12. Certified Forest Area
13. Environmental flow
14. Floodplain / Riparian Reserve

Fig. 4. Examples of place-based tools for protecting freshwater ecosystems, set within a catchment context. Used with permission from Stuart Blanch.

Environmental flows

Environmental flows are an increasingly important example of a place-based strategy integrally tied to the larger catchment. The term 'environmental flows' in essence refers to instream water flows 'needed to sustain the ecological health of river ecosystems and the array of goods and services they provide to society' (Richter 2010). The flows are measured at one or more locations in a target freshwater system, but management of flows can occur within a system – such as at a dam location – or anywhere in the upland catchment where water withdrawals and returns are contributing to an ecologically unsustainable flow regime.

The concept of managing flow regimes for environmental goals extends back as far as the 1940s, but modern approaches to determining environmental flow prescriptions date largely from the 1980s to the present (Tharme **2003; Petts 2009**). Over 200 different methodologies exist, but most have in common the integration of the best available physical and biological data with input from expert aquatic ecologists, hydrologists, geomorphologists, chemists, and other scientists as well as stakeholder groups (O'Keeffe 2009). The main output is the determination of a flow allocation for the environment (Tharme 2003).

Despite the proliferation of environmental flow methodologies, the water management sector around the world has been slow to adopt and implement them (O'Keeffe 2009; Richter 2010). One reason, according to Richter (2010), is that environmental flows are often associated with species conservation and recre-

ational fisheries, rather than with providing a broad range of ecosystem services. Ecosystem services are defined simply as the benefits that people derive from natural ecosystems. Rather than identifying specific flow allocations for the environment, Richter proposes defining 'sustainability boundaries' within which flows should be managed. This approach has the benefit of providing more flexibility to water managers and stakeholders, and of reframing discussions away from people *versus* the environment and toward benefits accrued to people *and* the environment (Richter 2010). Indeed, many recent environmental flow initiatives have been framed in terms of ecosystem services benefits. The World Bank states that 'Environmental flows are really about the equitable distribution of and access to water and services provided by aquatic ecosystems (Hirji & Davis 2009), and the Millennium Ecosystem Assessment identifies environmental flow allocations as a key strategy for maintaining wetlands services (MEA 2005b). The adoption of requirements for environmental flow assessments by less developed countries like South Africa, Tanzania, and Zimbabwe is one indication that environmental flows are increasingly seen through the lens of societal benefits (O'Keeffe 2009). Tanzania's 2002 Water Policy, for instance, which prioritizes water for the environment second only to water for basic human needs, explicitly identifies water as a 'source of natural capital' (United Republic of Tanzania 2002). South Africa's water policy has become a model for the rest of the world, including some more developed nations, and much of the seminal flows research originated and continues to be produced there.

As environmental flows are increasingly offered as a tool for sustainable development and poverty alleviation, as well as for climate change adaptation (Dyson *et al.* 2008; Hirji & Davis 2009), the strategy's origins in species conservation and recreational fisher-

Table 1. Ecosystem services provided by or derived from wetlands. Taken from the Millennium Ecosystem Assessment (MEA 2005b).

Services	Comments and Examples
Provisioning	
Food	production of fish, wild game, fruits, and grains
Fresh water	storage and retention of water for domestic, industrial, and agricultural use
Fiber and fuel	production of logs, fuelwood, peat, fodder
Biochemical	extraction of medicines and other materials from biota
Genetic materials	genes for resistance to plant pathogens, ornamental species, and so on
Regulating	
Climate regulation	source of and sink for greenhouse gases; influence local and regional temperature, precipitation, and other climatic processes
Water regulation (hydrological flows)	groundwater recharge/discharge
Water purification and waste treatment	retention, recovery, and removal of excess nutrients and other pollutants
Erosion regulation	retention of soils and sediments
Natural hazard regulation	flood control, storm protection
Pollination	habitat for pollinators
Cultural	
Spiritual and inspirational	source of inspiration; many religions attach spiritual and religious values to aspects of wetland ecosystems
Recreational	opportunities for recreational activities
Aesthetic	many people find beauty or aesthetic value in aspects of wetland ecosystems
Educational	opportunities for formal and informal education and training
Supporting	
Soil formation	sediment retention and accumulation of organic matter
Nutrient cycling	storage, recycling, processing, and acquisition of nutrients

ies may become increasingly distant. Nonetheless, the needs of freshwater ecosystems, however those needs are defined, remain at the core of virtually any environmental flows methodology. Larger societal goals, then, may ultimately pull freshwater biodiversity conservation more directly into the mainstream despite the fact that the strategy was originally designed with conservation in mind.

Ecosystem Services Protection
The case of environmental flows highlights the strong interest of both the conservation and development communities in ecosystem services. The concept of ecosystem services has gained global attention with the publication of the Millennium Ecosystem Assessment (MEA 2005a). The MEA's identification of different services includes a prominent number tied to freshwater systems (Table 1) (MEA 2005b). Most of these freshwater services relate to water rather than to biotic resources, and that is where much of the focus of conservation organizations has been to date. But maintaining water resources can have benefits for freshwater biodiversity as well.

Conservation groups and research institutions are assessing freshwater ecosystem services for particular places, attempting to value them, and then using that information to influence management and policy decisions. For instance, the Natural Capital Project – a collaboration among Stanford University's Woods Institute for the Environment, University of Minnesota's Institute on the Environment, The Nature Conservancy, and World Wildlife Fund – incorporates modeled assessments of water provision into its work in a number of regions around the world, including Tanzania's Eastern Arc Mountains. The Natural Capital Project selected the Eastern Arc Mountains as a pilot landscape because its exceptionally biodiverse forests, under threat from encroaching agriculture, unsustainable timber harvest, and fire, supply critical services in the form of timber products, climate stabilization, and water resources (Burgess *et al.* 2009). In particular, water resources originating in the mountains generate hydropower and provide drinking water, and disruptions to the reliability of those resources have repercussions on Tanzania's downstream population centers. Work is currently underway to compare areas of high water yield, areas important for carbon storage, and areas supporting key terrestrial species groups. In effect, the presence of so-called 'water towers' – mountains that are critical to supplying downstream fresh water (Viviroli

et al. 2007) – are employed to argue for protection of overlapping terrestrial biological priority areas. It is important to note that this assessment and others like it have relied heavily on modeled data, and that hydrology models in particular have proved challenging to construct, so the results should be understood in that context.

The Natural Capital Project's work is just one example of many ongoing efforts to develop ecosystem services-based arguments for conserving areas of importance to biodiversity. In another study, Egoh *et al.* (2009) mapped several ecosystem services in South Africa and found that the need to maintain water flow regulation and surface water supply could help to justify conservation of natural habitats in the fynbos and the Indian Ocean coastal belt. Although these types of analyses are typically motivated by an interest in protecting terrestrial species and habitats, an important freshwater biodiversity component could conceivably be incorporated by identifying freshwater hotspots – data permitting – and then mapping the upstream catchment areas critical for maintaining the flow regimes of those specific river reaches, lakes, or wetlands. Even ecosystem services assessments focused specifically on measuring the benefits of freshwater systems (e.g. Jogo & Hassan 2010) have generally quantified provisioning and regulating services without considering how freshwater biodiversity in particular might be targeted for protection, or whether strategies for protecting those services actually convey protection to freshwater species. Nonetheless, the substantial focus on water resources within many of these projects suggests that freshwater species and habitats could benefit indirectly from policy initiatives intended to protect the reliability of water supplies and the availability of wetlands products if areas of high priority for species and habitat conservation overlap those of high importance for ecosystem service production.

Market transformation
Strategies built around ecosystem services, environmental flows, and protected areas are all, in a sense, bottom-up approaches. That is, geographic areas of interest from a biodiversity or services perspective are identified first, and then strategies are developed to mitigate or protect against current or future threats. Another emerging strategy, the reduction of water footprints through market transformation, takes a more top-down approach, identifying drivers first and subsequently prioritizing geographies based on

Fig. 5. Average per capita water footprint of national consumption (m3/capita/yr). From Mekonnen and Hoekstra 2011. Used with permission

where drivers are having the greatest impact and leverage opportunities are highest.

Market transformation is in essence the attempt to influence key leverage points in global supply chains of priority commodities so that the ecological footprints of those commodities are reduced. Leverage points can be producers, processors, retailers, and consumers. Working with companies to reduce their carbon footprints is a prominent example of market transformation. Another quickly emerging focus of market transformation aims to reduce water footprints.

Many people are introduced to the water footprint concept through maps of national-level footprints. A nation's 'water footprint of national consumption' is defined as 'the total amount of fresh water that is used to produce the goods and services consumed by the inhabitants of the nation' (Fig. 5) (Mekonnen & Hoekstra 2011). As defined by Mekonnen and Hoekstra (2011), the measure consists of two components: internal and external water footprints of national consumption. The internal water footprint is 'the use of domestic water resources to produce goods and services consumed by the nation's population.' The external water footprint is 'the volume of water resources used in other nations to produce goods and services consumed by the population in the nation under consideration.' Countries with exceptionally high populations, like China and India, may have relatively low water footprints per person but when aggregated across the entire population, the footprints grow substantially.

There are also production footprints, which is where work on water footprints largely originated. A company's water footprint is the volume of fresh water used to make all of its products. Each product in turn has its own water footprint, comprised of the footprints of each step in the supply chain. Production footprints for one or more industries can also be calculated for a defined geographic area, like for export cut flowers produced in the drainage basin of Kenya's Lake Naivasha (Mekonnen & Hoekstra 2010). From a biodiversity perspective, reducing production footprints may be equally if not more critical than reducing consumption footprints, because a focus on production footprints allows targeting the largest water users in the places that need the greatest protection. The greatest proportion of water use by far comes from agricultural production, which accounts for 70% of all freshwater used globally, from both surface and groundwater sources (FAO 2010). Industrial production is second, at 20%. With these numbers in mind, many in the conservation community are identifying global commodities like cotton with high potential for improved water use efficiencies, and are working with companies to identify where water can be used more efficiently within their product supply chains. This provides a potential win-win situation, because companies can benefit economically as well as by reducing their water-related risk.

Market transformation initiatives focused on water are largely in the developmental phase. One effort, the Alliance for Water Stewardship (AWS), aims to design standards and a certification program for ma-

jor water users around the world (http://www.allianceforwaterstewardship.org/). This certification program would be roughly akin to those for forests (e.g. Forest Stewardship Council) or marine fisheries (Marine Stewardship Council). One proposed environmental criterion of the AWS standard involves ensuring environmental flows in the systems affected by major water users (AWS 2013). Achieving this objective, then, will require going beyond reducing overall water footprints to consider *when* water is abstracted in addition to *how much*. Furthermore, from biodiversity, social, and cultural perspectives, some freshwater systems will be more important than others. However high value systems are identified, the existence of such systems suggests that *where* water is abstracted should be considered in addition to when and how much, and that more stringent standards may be appropriate where especially highly-valued systems could be impaired. Additional potential objectives related to water quality and governance would also need to take these high value systems into account.

Another complicating factor for water market transformation work is that water use must be assessed within a drainage basin context. The impact of a single company or farmer's water use in a given basin may be small, but the cumulative impact across all users can be large. Standards might be adjusted, then, based on the basin-wide situation, with even an efficient water user potentially failing to achieve certification within a water-stressed basin. Certifications aside, there is also the risk that market-driven reductions in water use could have unintended consequences; for instance, a sugarcane farmer might reduce her water use but compensate by using more pesticides, or the next farmer downstream might use the extra available water for his crops. These nuances underscore that even when market transformation initiatives are working with global companies, water is ultimately local and must be managed as such. Global or regional market-based initiatives, then, must be integrated with on-the-ground management, incorporate indicators at both the watershed and production site scale, and require careful monitoring of biodiversity and ecosystem outcomes. These complications point to a key difference from efforts to reduce carbon footprints, where reductions anywhere produce a global benefit.

Climate Change Adaptation

Climate change mitigation may be global, but climate change adaptation – 'developing active strategies that increase system resilience by explicitly incorporating

the effects of climate change' (Matthews *et al.* 2009) – is decidedly local. In many places, climate change is already having measurable impacts on water quality, quantity, and timing – parameters that shape freshwater systems, and to which freshwater species are by and large adapted (Le Quesne *et al.* 2010). Of these parameters, changes in the timing of flows are potentially the most concerning from a freshwater ecology and biodiversity perspective (Poff *et al.* 2002), but discussions around climate change impacts have only begun to focus on these parameters in earnest.

In general, levels of uncertainty around climate change impacts on water are higher than around impacts to ambient air temperature (Matthews & Wickel 2009). But even if we cannot know at present the direction and magnitude of change for any given system, there is historical precedent to suggest that as the reliability of water resources is reduced, human communities often respond with solutions that only further exacerbate existing stresses on freshwaters. Such 'fixes' can include construction of new dams and other relatively permanent infrastructure, resulting in myriad impacts including reduced connectivity of already impaired systems – which in turn diminishes dispersal opportunities for aquatic species facing novel environments. These responses, which typically fall under a traditional 'hard-path' approach to water management, have been termed 'maladaptation' (Gleick 2002; Barnett & O'Neill 2009). Climate change mitigation strategies involving a shift to low-carbon sources of energy like hydropower would also compound disturbances to freshwater systems (Le Quesne *et al.* 2010). In essence, climate change adaptation accepts that the future will be different from the present and attempts to find ways to adapt to those changes. Freshwater climate change adaptation specialists have begun to formulate general recommendations for water resource managers, development banks, the conservation community, and others with a stake in the world's 'linked socio-hydro-ecologic systems' (Matthews *et al.* 2009). Matthews & Le Quesne (2009) provide one list of guidelines (Table 2). Most of these recommendations target policy as much as, if not more, than science and management. But there remains a strong role for biological scientists and on-the-ground managers, particularly in designing and implementing strategies to reduce non-climate pressures, in developing monitoring systems, and in evaluating the appropriateness and feasibility of managed relocations (Minteer & Collins 2010).

Table 2. Guidelines for freshwater climate change adaptation. From Matthews & Le Quesne 2009. Used with permission.

- Develop institutional capacity
- Create flexible allocation systems and agreements
- Reduce external non-climate pressures
- Help species, human communities and economies move their ranges
- Think carefully about water infrastructure development and management
- Institute sustainable flood management policies
- Support climate-aware government and development planning
- Improve monitoring and responsiveness capacity

Managed relocations, which has and continues to be controversial (Ricciardi & Simberloff 2009), is gaining a higher profile as the conservation community grapples with the likelihood that many species – especially those inhabiting freshwater 'islands' – may be unable to disperse on their own to new habitats. While the largely unpredictable outcome of moving species and populations outside their historic ranges may argue against such translocations, an alternate view suggests that historic habitats and communities may cease to be meaningful constructs within future climate conditions. Freshwater fish and fisheries scientists and managers are well-equipped to contribute to this discussion, given the long record of well-documented fish introductions and extensive research into the structure and function of aquatic communities.

HOW FISH AND FISHERIES EXPERTS CAN CONTRIBUTE

Scientists and managers have a role not just in developing and implementing climate change adaptation interventions, but in doing the same for all of the other freshwater conservation strategies mentioned here as well. Alongside developing and implementing strategies is the need to evaluate them. Unfortunately, though perhaps not surprisingly, few empirical studies have rigorously evaluated whether these and other strategies are achieving their conservation goals. This gap is far from exclusive to freshwater and extends across all biomes (MEA 2005a).

The most conclusive evaluations would examine the counterfactual to determine if outcomes would be significantly different in the absence of a conservation intervention. This standard is routinely applied within the public health, education, and medical sectors, but it represents an exceptionally high bar for the conservation community, since the natural world offers few perfect controls. Nonetheless, a small but growing number of researchers and donors is calling for the conservation community to engage in so-called evidence-based conservation, without letting the perfect become the enemy of the good in terms of study design (Ferraro & Pattanayak 2006; Bottrill *et al.* 2011). Even if a rigorous evidence-based evaluation is out of reach for most conservation programs or interventions, other types of monitoring or evaluation may be appropriate and feasible. These range from status assessments of how social and environmental conditions change over time, to management effectiveness assessments, to performance measurements of individual projects or programs (Pailler *et al.* submitted). Each of these types of monitoring and evaluation requires field data and careful interpretation, and there is ample room for contributions by experts.

Here we provide a few ideas as to how fish and fisheries experts can contribute to making the strategies presented here more effective, from design all the way through to monitoring and evaluation.

Protected areas

Information on fish communities, populations, and life histories will be essential for identifying where new protected areas should be located, how they should be designed, and for identifying the species and system attributes for which the reserves should be managed. New protected areas will need baseline inventories conducted, and both new and existing reserves will require monitoring plans to assess whether they are meeting their goals, and to facilitate adaptive management if they are falling short. Ideally, any monitoring would involve capacity building of protected area managers, staff, and possibly also community groups.

Environmental flows

Designing and implementing environmental flows will require similar kinds of inputs from fish experts as protected areas, with a particularly strong focus on collecting additional data on species distributions and life histories, and on monitoring and adaptive management. Environmental flows interventions, by nature of their controlled nature, may lend themselves more strongly to impact evaluation than other strategies.

Ecosystem services protection

Water and carbon are currently receiving the most attention in ecosystem services assessments, perhaps because modeling them in a geographic information system (GIS) environment is tractable, though as yet not entirely reliable from a hydrology perspective. There is no doubt that freshwater fisheries are highly valuable and chronically undervalued (UNEP 2010). As ecosystem services projects move to incorporate freshwater fisheries, fisheries experts and particularly population biologists will be in high demand. Perhaps even more challenging will be assessments of supporting services like nutrient cycling and primary production, two other freshwater growth areas.

Market transformation

Working with companies and financial institutions to reduce their production footprints will require knowing which areas within a production landscape or watershed require the highest levels of care. Identifying these areas – so-called high conservation value freshwaters – is akin in many ways to traditional freshwater conservation planning, with some key differences. First, high conservation values may include not only biodiversity attributes but also areas that supply critical ecosystem services like fisheries, as well as areas of cultural importance. Additionally, because maps of high conservation value freshwaters will not exist at appropriately small scales for most regions, assessments may be commissioned on a case-by-case basis, in which instance the region of analysis would be determined in part by the type and scale of production activity and its potential downstream or even upstream impacts. Fish experts may be called upon not only to help identify high conservation value areas for fish and fisheries, but also to contribute to studies to determine the impacts over space and time of different commodity production practices. The potential impacts of different practices go beyond water use and consequent changes to the flow regime to also include changes to water quality, nutrient and sediment regimes, direct habitat alteration, and the possible spread of non-native species.

Climate change adaptation

Vulnerability assessments are a key component of climate change adaptation work, requiring the input of fish experts and other freshwater scientists and managers. In essence, a vulnerability assessment uses scenario analysis to identify those ecosystems that are most sensitive to and at risk from change (Le Quesne *et al.* 2010). Fish and fisheries experts would help to describe aquatic ecosystems and associated services; identify ecosystem objectives and thresholds of concern; describe the current situation and identify ecosystem sensitivities; and design adaptation strategies (Le Quesne *et al.* 2010).

CONCLUSIONS

The world's freshwater species have never been in greater peril worldwide, and freshwater biodiversity conservation is not a particularly high priority, even within the conservation community. However, there has never been so much interest as there is now in water resource issues, particularly as they relate to private sector risk and ecosystem services. Protecting and managing water supplies is central to many of the conservation strategies that are gaining traction, and there are often linked or secondary benefits to freshwater ecosystems and the species they support. These benefits cannot be assumed, though. For instance, the service of carbon sequestration through afforestation may be in direct conflict with services related to water supply and terrestrial biodiversity (Chisholm 2010). Freshwater species, presumably adapted to the natural flow regime, may be missing from the discussion altogether unless they provide a service of their own, even though actions taken as a result of the assessment could have ramifications for the species' future survival.

Freshwater fish and fisheries experts, working within and outside the conservation community, must ensure that freshwater systems and species are integrated into existing and emerging conservation strategies. One way of facilitating that integration is to have the best available information on hand. Freshwater species and systems have historically been omitted from conservation planning and conservation strategies in large part because information describing them was lacking. Freshwater data may still lag behind those for terrestrial systems, especially in the less devel-

oped world, but they have now reached a level of detail and comprehensiveness such that freshwater systems should at least have a seat at the table. Freshwater fish and fisheries information remains critical to effective project design, implementation, and management – and not only for freshwater-focused projects. The strategies may be changing, but the goal of conserving freshwater fish and fisheries remains paramount.

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Advances in African Aquatic Biodiversity Informatics

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ABSTRACT

COETZER, W. & SKELTON, P.H. 2013. 'Advances in African Aquatic Biodiversity Informatics'. In J. Snoeks & A. Getahun (eds), *Proceedings of the Fourth International Conference on African Fish and Fisheries, Addis Ababa, Ethiopia, 22-26 September 2008*. Tervuren: Royal Museum for Central Africa, 'Zoological Documentation Online Series', pp. 21-30.

Thirty years ago accurate, scientific maps depicting the distributions of African animals and plants were uncommon and difficult to produce. Today such maps can be generated easily using a plethora of digital tools and online databases. African biodiversity information has never been more accessible than it is now, but more work is required to increase the amount of online biodiversity information, and to improve the quality of information.

This account explores the development of biodiversity informatics and its application to research in African ichthyology. We trace the progress from unwieldy specimen catalogues, through early databases and geographic information systems to custom biodiversity databases and the global online biodiversity databases that are now the state of the art. The World Wide Web has revolutionized our science because it has allowed us to communicate instantly and precisely using our traditional metaphor. At a time of accelerating global change the need to mobilize African biodiversity information has never been more urgent.

Keywords: biodiversity information, data standards, data quality, biodiversity conservation

INTRODUCTION

Biodiversity Informatics is the application of informatics to recorded and yet-to-be-discovered information specifically about biodiversity, and the linking of this information with genomic, geospatial and other biological and non-biological datasets (OECD 1999). Several authors have defined and nuanced the meaning of 'biodiversity informatics' (Bisby 2000; Soberón & Peterson 2004; Johnson 2007; Sarkar 2007). The concept can be extended as Biodiversity and Ecosystem Informatics. In its basic form, the information consists of specimen records of plants and animals, usually originating from preserved specimens in natural history museums. The kinds of queries or analyses range from opportunistically extracting specimen locality information to running an advanced ecological niche modelling algorithm to discover unexplored localities that may harbour new specimens. A list of more than 600 current projects related to biodiversity informatics can be found on the website of the collaboration known as Biodiversity Information Standards (formerly the Taxonomic Database Working Group of the International Union for Biological Sciences, which has met since 1985) (Anonymous 2007).

There is a distinction, in the level of biological organisation, between biodiversity informatics and bioinformatics. The latter, specialized field uses algorithms to compare gene sequences through computationally intensive permutations of base-pairs. On the other hand, biodiversity informatics includes the capture, storage, analysis, synthesis, reporting, use and sharing of biodiversity information (e.g. taxon names, specimen records, observations, images and literature) in such a way as to exploit the natural relationships and structure in the information. Qualitative, linked genetic information is included.

To manage biodiversity information a custom-designed relational database is required, in which specimen records can be captured accurately, precisely, and in a timely manner, and which can be used to extract information and conduct meaningful analyses. Specify Software (Kansas University Natural History Museum) and Biótica (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Government of Mexico) are examples of biodiversity databases designed specifically for the purpose of handling biodiversity information associated with specimens. All too often these data are captured haphazardly, inaccurately and with no control over data quality, in spreadsheets or unstructured databases,

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or in static copies of data extracted from structured biodiversity databases. This makes it difficult to re-unite, integrate, compile, summarise and analyse the biodiversity information, or to contribute the data to online repositories of biodiversity information, such as the Global Biodiversity Information Facility (GBIF). The reason that we record biodiversity information, and the reason that we need to design proper information systems for this purpose, and work with accuracy and precision, will ultimately be traced to the planet's biodiversity crisis. Biodiversity scientists are trying to publish, in online databases, as many records of specimens and observations as is possible, to map the patterns of Earth's ailing biodiversity, and to support decision-making and conservation planning and action. Biodiversity information is also essential to answer the more academic questions arising in fields such as systematics, phylogeography and evolution.

In the last few years there have been a number of advances in African aquatic biodiversity informatics. In this paper we briefly describe the major technological advances that facilitated the development of the field of biodiversity informatics. We then highlight recent important African contributions to particular biodiversity informatics projects. We emphasize the importance of well-curated specimen collections and information, communication, data standards and data sharing.

AN HISTORICAL PERSPECTIVE

It has been suggested that the first human ideas that would eventually culminate in today's Geographic Information Systems were depicted in the famous caves near Lascaux, France, by Cro-Magnon hunters. These are thought to have communicated the migration routes of prey animals. The Egyptians illustrated nature in all her glory, and it comes as no surprise that the essence of what we do when we engage in biodiversity informatics is an act of communication. When, in 1815, Robert Dingley, an ensign of the Cape Corps, painted fishes on the banks of the Koonap River in the Eastern Cape, South Africa (Skelton & Skead 1984), he couldn't have known that almost 200 years later his paintings would be considered valuable observational records of the occurrence of two species of fishes at that particular place at that particular time. From this we can confidently settle the debate as to whether *Labeo umbra-*

tus (Smith 1841) (Cyprinidae) was a native species or had been introduced to the drainage system by human agency. For centuries we relied on individual illustrations or limited reproductions in books and journals to communicate biodiversity information. Information retrieval improved for those with access to good reference collections such as the Zoological Record, but it nevertheless required skill, time and knowledge to manage a library effectively. Today we use GPS instruments to record our precise locality ('to the nearest second'), take high-quality digital photographs of voucher specimens, vigorously catalogue our records in sophisticated software, and display all of this information on Google Earth in a matter of minutes.

The milestones of African freshwater fish systematics were summarized by Lévêque (1997) and more recently by Paugy (2010) and Skelton and Swartz (2011). Beginning with Linnaeus (1758) the first period extended until around 1850 and included a few significant publications such as those of Cuvier and Valenciennes (1828) and Andrew Smith (1841). In this period the first scientific descriptions of African freshwater fishes appeared, based on collections made by early explorers. The descriptions were basic, and while illustrations were included in some descriptions (e.g. Burchell 1822; Smith 1841), information on geographic distribution was elementary. The second phase, from 1850 to 1940, was a period of many discoveries and major catalogues, first that of Günther (1868) and later by Boulenger (1909-1916), who curated the freshwater fish collection of the British Museum, the main source of public information on African freshwater fishes. These works were supplemented by Boulenger's (1907) Fishes of the Nile, Pellegrin (1911), and in South Africa, the catalogue of Gilchrist and Thompson (1913, 1915). These advances in systematic knowledge allowed for some early syntheses of the patterns of fish distribution in Africa (e.g. Günther 1880; Weber 1897; Boulenger 1905; Pellegrin 1911; Nicols & Griscom 1917). Barnard's (1943) account of the fishes of the southwestern Cape was a landmark publication because it was an early effort to combine real systematic information on the growth and intraspecific variation of species with their distribution, plotted from museum collection records.

The period between the Second World War and the end of the 20th Century is marked by great growth in detailed knowledge of the freshwater fish fauna

at regional and national scales (e.g. Trewavas & Irvine 1947; Copley 1958; Jackson 1961; Daget & Iltis 1965; Greenwood 1966; Jubb 1967; Poll 1967; Bell-Cross 1976). The comprehensive Catalogue of the Freshwater Fishes of Africa (CLOFFA) was produced in four volumes (Daget *et al.* 1984, 1986a, 1986b, 1991). With respect to informatics there was increasing representation of museum specimens as points on maps (e.g. Thys van den Audenaerde 1964; Teugels 1986; Skelton 1987; de Vos 1995; Lévêque *et al.* 1990, 1992), and increasing application of analytical techniques to specimen records. The period ended as digital information and the internet were emerging as tools used by biodiversity scientists.

THE DEVELOPMENT OF BIODIVERSITY INFORMATICS

We owe our ability to execute complex biodiversity analyses to the development, in the 1970s, of relational databases. It was not until the 1990s, however, that specimen databases really became widely adopted in natural history museums. In the 1980s another revolutionary development came about in the form of GIS that could run on personal computers. Today most biodiversity databases are linked to a GIS platform that can be used to conduct powerful spatial analyses of biodiversity information. In the 1990s the World Wide Web made it possible to publish static species lists or collection holdings. Researchers could suddenly communicate with one another using biodiversity information. Richly formatted websites were created that included images and maps. At first these were static and required maintenance. In the last 5 years the power of even unskilled users has increased markedly due to the proliferation of online tools that combine the structure and data validation of databases with the reach of the web: as the data are captured in the database, so they become published (Scratchpads).

Two global products that were developed in the 1990s are the pillars of online information about all fishes, not only African freshwater fishes. The first of these is FishBase (Froese & Pauly 1998), which was originally available in 1995 as a published CD-ROM. FishBase was a pioneer in online species- and specimen information, and continues to provide current, multi-disciplinary information that is used across the continent of Africa. Aquamaps (Kaschner *et al.* 2010), a joint project of FishBase and SeaLife-

Base, is an online tool that can be used to perform exploratory ecological niche modelling without the need for separate species occurrence data, a modelling algorithm or even the skills to combine the two. Aquamaps illustrates how FishBase has kept abreast of technological innovation. The second global product is the Catalog of Fishes (Eschmeyer & Fricke 2011), which came online as early as 1998, and is the authoritative source of comprehensive taxonomic information on fishes.

Whereas the early 1990s were interesting times for publishing small amounts of biodiversity information online in any manner at all, the present challenge we face is to bring structure, standards and meaning to the burgeoning online biodiversity information repositories, and to integrate them or make them interoperable. Much progress has been made in the development of biodiversity information standards. A simple example will be used to explain the general meaning of standards in biodiversity information. Typically, field names differ between biodiversity databases. For example, one database might include a field named 'ScientificName' while another database may store the same kind of information in a field named 'TaxonName'. Rather than relying on agreements between people to name database fields consistently (an obviously unmanageable task), we introduce a standard set of field names, or terms, that we agree to map to our differently named fields. Every time we export a dataset, our fields will be automatically renamed to comply with the agreed terms. This allows us to publish a combined dataset containing the same kinds of information merged into the correctly-named fields, even if our original databases still have differently named fields. The widely used Darwin Core is such a set of common terms (Wieczorek *et al.* 2009).

The establishment of the Global Biodiversity Information Facility in 2002 was another significant milestone in the development of Biodiversity Informatics. Before 2002 online specimen records were differently formatted and hard to find because they were distributed throughout the web on static websites. There are now more than 260 million specimen records available through the GBIF Data Portal. Queries are quick to return records contributed by thousands of providers across the globe, all instantly mapped and consistently formatted according to the Darwin Core standard. Significantly, the biodiversity information presented by the GBIF data portal originates directly

from original contributors, and is not aggregated centrally. This means that the information is dynamic and reflects the changes made when the contributing databases are updated. With its philosophy of 'free and open access to biodiversity data', GBIF also put paid to the concept of proprietary ownership of data, though sensitive data related to endangered species can still be protected.

Information pertaining to species as entities has enjoyed the same attention afforded to specimen records. During the International Year of Biodiversity, in 2010, the Catalogue of Life contained about 1.25 million records of species. This collaboration, as well as the Integrated Taxonomic Information System, Encyclopedia of Life, the International Barcode of Life (iBOL) and the Biodiversity Heritage Library, among others, are now at the forefront of 'big' biodiversity informatics. That these global information networks of formally participating institutions and governments interact meaningfully with one another represents another milestone in the development of data integration and interoperability in biodiversity informatics.

AFRICAN NODES OF GBIF

In 2008 the South African Biodiversity Information Facility was the only established GBIF participant on the African continent, but strong initiatives were on the horizon in Ghana, Tanzania and Kenya. Come 2012, the African contribution to GBIF will be broad-based and more dynamic than ever, with nodes now being established in Benin, Burkina Faso, Cameroon, Equatorial Guinea, Guinea, Madagascar, Mauritania, Togo and Uganda. In addition to these country nodes of GBIF, organization nodes have also been established by the Endangered Wildlife Trust (South Africa), the International Centre of Insect Physiology and Ecology in Kenya, and ARCOS, the Albertine Rift Conservation Society (United Kingdom and Uganda). The South African Biodiversity Information Facility (SABIF) currently has 8 data providers, of which the largest contributor of freshwater fish information (about 35,000 specimen records) is the South African Institute for Aquatic Biodiversity (SAIAB). The SAIAB specimens originate mostly from southern Africa, and are contributed to other online repositories as well, notably Faunafri (Paugy *et al.* 2008), an innovative, high resolution online GIS utility that displays freshwater fish information from across the African continent.

ADVANCES IN AFRICAN AQUATIC BIODIVERSITY SCIENCE AND BIODIVERSITY INFORMATICS

Effective conservation of freshwater fishes requires detailed information on the status and distribution of species. The advances in African aquatic biodiversity informatics are exemplified by a number of flagship projects, which we describe below. In addition to new collaborations within Africa, there are well established collaborations between Africans and scientists from further afield. For example, members of the Congo Project of the American Museum of Natural History are explaining the strange morphologies and mechanisms of evolution caused by the extreme hydrological characteristics of the lower Congo River (Markert *et al.* 2010). The project team includes scientists and students from New York, Kinshasa and Brazzaville.

The Atlas of Southern African Freshwater Fishes

Scott *et al.* (2006) developed an early example of the use of GIS to integrate data from several museum collection databases to produce distribution maps of southern African freshwater fishes. The Atlas of Southern African Freshwater Fishes (Scott *et al.* 2006) contained records from 19 museums across the globe. These records were either manually captured from hard-copy catalogues or were provided in digital format, and geo-referenced. Although generalized distribution maps had been published before, in the case of many species these were the first to be based on precise localities from museum records. The atlas was published in hard-copy and on CD-ROM.

The Maloti Minnow Conservation Plan

The Maloti minnow, *Pseudobarbus quathlambae* (Barnard 1938), is an endangered cyprinid from high-altitude streams in the Drakensberg and Maloti mountains of the Lesotho highlands. The Lesotho Highlands Development Project (LHDP) involves the construction of several large, interconnected impoundments for the supply of electricity and water to Lesotho and South Africa. In Phase 1 of the LHDP two large dams, the Katse Dam and the Mohale Dam, were built on the Senqu branch of the drainage system, which drains into South Africa's Orange River. The LHDP was required to take steps to counter threats to the survival of the Maloti minnow, the only endemic fish species in the area affected by the LHDP. The

South African Institute for Aquatic Biodiversity was contracted to study the potential effects of the LHDP on the Maloti minnow between 1999 and 2002. Before the project began the species was known from only four localities: three low-order streams on the western edge of the watershed near the international boundary, and the Jordane River (Skelton 1987) (Fig. 1). New populations were discovered in the Sani River during a preliminary study (Skelton & Molofo 1989), and, significantly, in the Matsoku river, a population that was to be affected by a diversion weir in Phase 1 of the LHDP. The LHDP would therefore directly affect two *P. quathlambae* populations. A conservation programme was commissioned that included a study of the distribution, biology, ecology and genetic status of the Mohale population, a comprehensive survey of the species throughout Lesotho, and an action plan and programme to conserve the Mohale population. The habitat of the Mohale population of *P. quathlambae* would be partly drowned by the Mohale impoundment and the population was threatened by the likely introduction of alien species via the water transfer tunnel between the Mohale and the Katse impoundments. One important discovery during this study was that the Mohale population is sufficiently genetically distinct to warrant full species status (Swartz 2005). The Mohale population therefore required separate conservation evaluation and action, and it was later determined to be Critically Endangered (Tweddle *et al.* 2009). Part of the action plan (Skelton *et al.* 2001) required identifying suitable sanctuary streams in Lesotho to which fish

could be translocated from the Mohale population. This was only possible after critical habitat characteristics had been identified using detailed existing distribution data. Figure 1 is a summary of the conservation plan of the Maloti minnow. This project illustrated how the analysis of well-managed specimen information encapsulating the various branches of natural science can facilitate important practical conservation policies and management.

The Freshwater Ecoregions of Africa and Madagascar

Conservationists and the major international governmental and non-governmental organizations require the vast amount of available biodiversity information to be analyzed, synthesized and summarized in order to focus and prioritize conservation attention and actions. The concept of an 'Ecoregion' – a large area of land or water containing a distinct assemblage of natural communities, and that of a 'Bioregion' – a complex of ecoregions that share a similar biogeographic history – are intended to facilitate large-scale assessment and understanding for the purpose of conservation planning and action. Continent-wide knowledge of African freshwater fauna and flora had not been considered sufficiently consistent to allow for the demarcation of such regions. Thieme *et al.* (2005) therefore used freshwater fish distribution as an interim proxy to define the aquatic ecoregions and bioregions of Africa. This ecoregion study was completed prior to the Pan African Freshwater Biodiversity Assessment described below, and relied on the compilation of freshwater fish information and distributions by individual experts.

The IUCN Pan-African Freshwater Biodiversity Assessment

Freshwater ecosystems are among the most transformed on the planet (Vörösmarty *et al.* 2010). Pressures to develop freshwater resources even further (Wetlands International 2010) are likely to increase dramatically as climate change causes rainfall in many parts of Africa to decrease (Vörösmarty *et al.* 2010; de Villiers & de Wit 2010). Freshwater is not only a precious resource for human life, but a medium for life itself (Palmer 2010; Vörösmarty *et al.* 2010). To guard against further deterioration of a resource so vital to human life and biodiversity, we need information as to the present conservation status of the key freshwater species that allow ecosystems
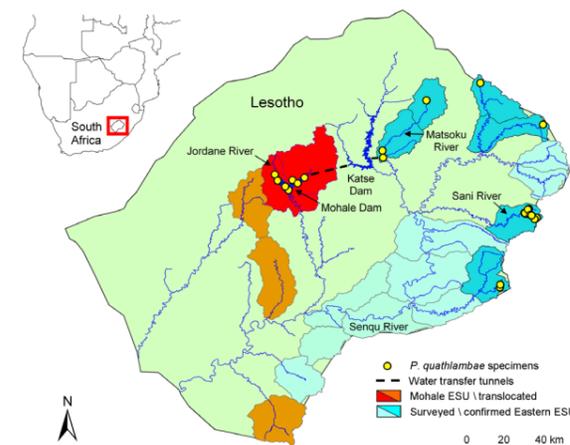
Fig. 1. The known distribution of, and conservation plan for, *Pseudobarbus quathlambae*. All coloured catchments were surveyed for minnows during the LHDP Maloti minnow project. ESU = Evolutionarily Significant Unit.

to function. To this end the South African Institute for Aquatic Biodiversity and several partner organizations collaborated with the IUCN to assess 355 species of freshwater fish species in southern Africa (excluding the cichlids of Lake Malawi) (Darwall *et al.* 2009). Aquatic plants (519 species), Odonata (272 species), molluscs (116 species) and crabs (19 species) were also assessed by various specialists. Biodiversity information was captured in the Species Information Service: Data Entry Module (IUCN), a sophisticated biodiversity database designed to store detailed information in hundreds of fields related to taxonomy, biology, distribution, utilization and the particular threats faced by each species. A distribution map of each species showed the river basins from which confirmed museum specimens had been collected. Basins that were thought to contain specimens, even if none had been collected, were also recorded. The ultimate objective was to mobilize this information for use by anyone required to assess the potential risk associated with infrastructural developments affecting water courses, waterbodies and freshwater ecosystems in southern Africa. The IUCN and its regional partners have replicated this work in other regions e.g. West Africa, East Africa and North Africa (Smith *et al.* 2009; Darwall *et al.* 2005; García *et al.* 2010).

The species maps were overlaid and the information
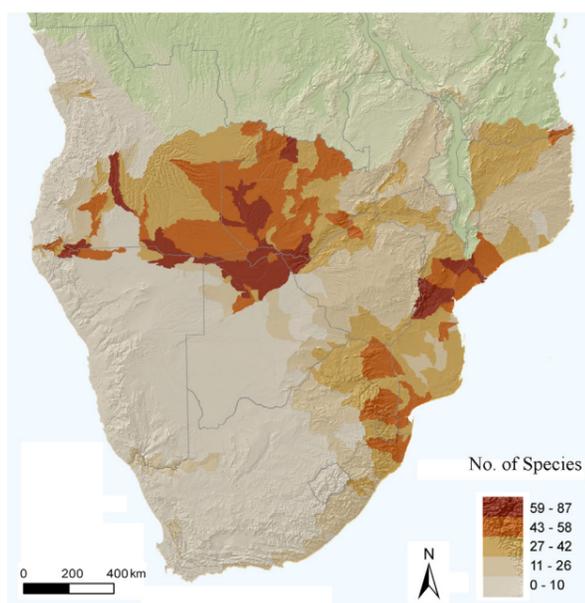
Fig. 2. The species richness of freshwater fishes in southern Africa. Source: IUCN\SAIAB Southern Africa Freshwater Biodiversity Assessment (Tweddle *et al.* 2009).

summarised to derive composite maps of standard biodiversity indices e.g. species richness (Fig. 2). The distribution of classes of species, such as those that are Threatened or Critically Endangered, could then be expressed. Using this African aquatic biodiversity information, similar analyses can be done for any individual catchment where development might be planned, making this an essential tool for assessing conservation status and impact, and for planning to mitigate impact.

The Freshwater Ecoregions Project and the IUCN Project worked on different spatial scales, but nevertheless showed us how collaboration and communication between experts can develop into collaboration between experts sharing a large amount of standardised biodiversity information. This enabled the development of a more refined product, and is an indication of how we will work with biodiversity information in the future. These projects also highlighted how rapidly biodiversity informatics has developed and continues to develop, which underscores the importance of staying abreast of innovations. Arguably the molecular focus of biodiversity informatics is the most innovative development of recent years.

The African Fish Barcode of Life Project

The global biodiversity crisis identified by the Rio Convention on Biodiversity in 1992 precipitated a number of large-scale initiatives to assess biodiversity, such as the Global Taxonomy Initiative. The task of discovering, identifying and classifying species is, however, an overwhelming one for a restricted and decreasing pool of taxonomists. One response to this 'taxonomic impediment' is to use molecular techniques to assist in identifying organisms through the 'barcode' sequence of the Cytochrome Oxidase I gene (Hebert *et al.* 2003). The International Barcode of Life Project (iBOL) is now described as the largest biodiversity genomics initiative ever undertaken. The Barcode of Life Data System (BOLD) (Ratnasingham & Hebert 2007) is an essential part of the project. In 2008 it contained the barcodes of over 1 million specimens and 93,000 species, including nearly 8,000 fish species (63,550 individual barcodes). A key aspect of barcoding is that each record must be supported by a voucher specimen in a recognized collection. This link to museum collections enhances the scientific value of the barcodes and establishes a powerful link to applied research. Properly and precisely recording

the physical (specimen) origin of molecular information, in the original contributing museum biodiversity database, is of paramount importance to ensuring that the published gene sequence will be easily and correctly kept inextricably linked to any changes made to the voucher specimen record (e.g. when specimens are redetermined). The BOLD is linked to GenBank and to other major biodiversity projects, such as the Encyclopedia of Life. The iBOL and the Convention on Biological Diversity have entered into a Memorandum of Understanding that establishes a formal framework of cooperation designed to further common goals.

The iBOL has several subprojects including one that seeks to barcode all fishes (www.FishBOL.org). Fish-BOL is active in Africa as well, with several projects on marine and freshwater species (Swartz *et al.* 2009). To date 1,264 species (14%) of the 8,980 African species have been barcoded. Barcoding is proving to be useful for identifying specimens collected in poorly explored regions such as the Congo basin and Angola (Lowenstein *et al.* 2011).

THE FUTURE

Organizing today's deluge of biodiversity information is difficult enough with today's technology, but what of the future flood of biodiversity information and future technology? Recording and analyzing biodiversity information will become increasingly automated, but the meaning and interpretation of results will still depend on how rigorously we design individual information systems, and whether humans will be able to use these systems easily. There are significant challenges, such as the inadequacy of traditional Latin names as unique and persistent identifiers of taxa (Cryer *et al.* 2009), and moving the official description and naming of species from paper to the digital medium (Pyle *et al.* 2008; Penev *et al.* 2010). In the intelligent information systems of the future (Michener *et al.* 2007), semantic integration will allow web services to do a lot of our work for us. A web service is defined as a software system designed to support interoperable machine-to-machine interaction over a network (World Wide Web Consortium). A web service requires the data that it will harvest to be standardized. The GBIF data portal makes several web services available to users exploring biodiversity information. One such web service is the 'occurrence density data service'. The GBIF data portal explains that this web service 'returns summary

counts of occurrence records by one-degree cell for a single taxon, country, dataset, data provider or data network'. What makes web services remarkable is that the information they provide is not aggregated in a single repository. Rather, the information is gathered from the nodes of a distributed network, and presented to us as if it were coming from a single source. All the analysis that would have been done by a human only a few years ago, in compiling occurrence records from disparate sources and analyzing the density of records per unit area, is now performed by a web service. Web services can be designed to perform all manner of manipulations of biodiversity data that were traditionally done by hand.

The Semantic Web is an evolving extension of the World Wide Web in which the semantics of information and services on the web is defined, making it possible for the web to understand and satisfy the requests of people and machines to use the web content. Rather than a 'web of documents', the semantic web will be a 'web of linked data' (World Wide Web Consortium).

Just as words such as 'browser' and 'home page' were new to us in the early 1990s, 'web service' and 'semantic web' are new to us now. But soon we will not think twice about the meaning of these concepts, as we use the web to answer our natural-language questions, 'speaking' to the web and it speaking to us. Our prediction is that amidst all the high technology the essence of our endeavours will remain an act of communication between human beings.

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Lake Tana's (Ethiopia) *Labeobarbus* Species Flock (Cypriniformes, Cyprinidae): a Future of Biodiversity Conservation and Sustainable Exploitation?

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ABSTRACT

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Lake Tana, the source of the (Blue) Nile, is situated in the north-western highlands of Ethiopia and harbours an extraordinary diversity of cyprinid fishes. While cyprinid fishes are common and abundant throughout the world's fresh water systems, the *Labeobarbus* species of Lake Tana form the only remaining intact species flock of large cyprinid fishes. Lake Tana and its *Labeobarbus* species flock provide(d?) an unique opportunity to study the selective forces driving speciation due, among others, to its relatively undamaged state. However, this undamaged state of the *Labeobarbus* species flock is seriously threatened by anthropogenic activities that have intensified over the past 30 years. Between the 1990s and early 2000s, *Labeobarbus* stocks decreased by 75%, most likely due to the increased fishing pressure after the introduction of a motorized commercial gillnet fishery. Many of the lake's *Labeobarbus* species are highly vulnerable to exploitation during their spawning aggregations and upstream migrations. Erosion due to poor land use might have also contributed to habitat degradation of the upstream spawning sites. Between 2000 and 2010 the commercial fishing fleet has expanded from 5-10 to 50-100 boats, but the *Labeobarbus* CPUE of the commercial fishery appeared to have declined a further ~50% over the same period. A (final) blow to the survival of the species flock will probably be the planned and realized (Rib River) irrigation dams in the spawning rivers.

Keywords: Africa, fisheries, adaptive radiation, irrigation dam, migration

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1. LAKE TANA

Lake features and geology

Several major river systems originate in the Ethiopian highlands. The most impressive river, however, is the (Blue) Nile which flows for 4,750 km from its source (Lake Tana) to the Mediterranean. The Nile River is principally fed by two great rivers, the White Nile (25%) and the Blue Nile (75%), which fuse at Khartoum, Sudan's capital city (Fig. 1). Over the last few centuries several European adventurers have travelled through Ethiopia in search for the source of the Nile. As early as the 1600s Portuguese priests established that the source of the Blue Nile is Lake Tana.

Lake Tana, Ethiopia's largest lake, is situated at an altitude of approximately 1,800m on the basaltic plateau of the north-western highlands of Ethiopia, 500 km north of the capital Addis Ababa. The oligomesotrophic [chlorophyll *a*, average 6.4 µg l⁻¹ (Dejen *et al.* 2004)], shallow lake (average depth 8 m, maximum depth 14 m) covers an area of ca. 3100 km². No apparent stratification occurs in the highly turbid lake. Several perennial rivers feed into Lake Tana (Fig. 2). The lake's ichthyofauna is isolated from the lower Nile basin by 40m high waterfalls, 30 km downstream from the Blue Nile outflow at Tissisat ('smoking water'). Rainfall, water level, water temperature and vertical transparency all follow seasonal patterns (de Graaf *et al.* 2004). Rainfall peaks in July-August, followed by a raise in the water level of the lake by 1.5 m, peaking in September-October (Fig. 3).

Lake Tana is situated within the Tana basin which covers an area of 16,500 km². The age of Lake Tana within the basin is uncertain. The lake might owe its present form to damming by a 50-km-long Quaternary basalt flow, which filled the exit channel of the Blue Nile River to a possible depth of 100 m. However, according to Chorowicz *et al.* (1998) the morphology of Lake Tana is not consonant with a lava-dammed, flooded river valley. Whether or not the lake was present before or after the blocking of the Nile outlet, the lava most likely created the waterfalls at Tissisat, isolating Lake Tana from the lower Nile drainage. Interestingly, deposits of lignitiferous sediments suggest that the Tana basin was occupied at least partly by a lake around 8 Ma ago, but it is unknown whether that lake survived the regional uplift during Late Miocene and Quaternary episodes (Chorowicz *et al.* 1998). A recent geological survey confirmed the suspected recent desiccation of Lake Tana during the later stages of the last Ice Age. A 12 m long sediment core taken in October 2003 from the deepest point (14 m) in Lake Tana includes a peat layer, at 935-980 cm depth, radiocarbon dated to 15,700-15,600 calibrated years ago (Lamb *et al.* 2007). The presence of peat, largely composed of the remains of Cyperaceae (probably *Papyrus*), indicates that water-level at the core site was about 9.5 m lower than presently.

Hydrology and ichthyology

Lake Tana's hydrological characteristics such as a high flushing time (6.1 years; Wudneh 1998, and references therein), small average depth (8 m; Wudneh 1998, and references therein), high seasonal changes in water level (high relative lake level fluctuation, seasonal (RLLF[s]), (Table 1) and a year round mixed water column categorise it as a seasonally pulsed system, an allotrophic riverine lake (Kolding, 1994; Jul-Larsen *et al.* 2003). In such water bodies biological productivity is mainly externally driven by nutrient inputs through seasonal fluctuations in water level and river inflow, including flooding of the lake margins and floodplains (Jul-Larsen *et al.* 2003). The influx of nutrients is often unpredictable and variable between years (high relative lake level fluctuation, annual (RLLF[a])) thus creating unstable environments. Pulsed, unstable systems (Table 1) are characterised by: a) highly variable biological productivity; b) fish communities dominated by ecologically flexible, unspecialised species with *r*-selected life histories; c) fluctuating and unpredictable natural
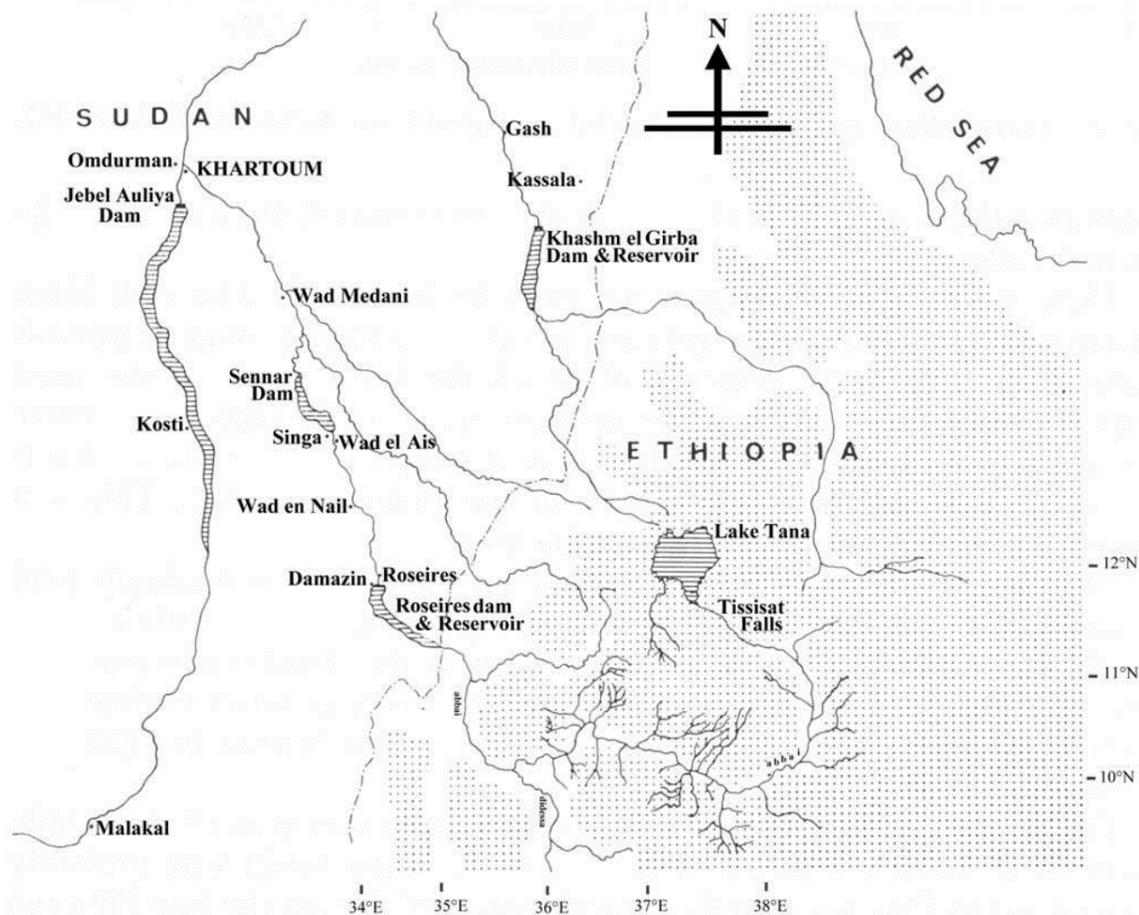
Fig. 1. Location of Lake Tana in the Blue Nile drainage system. Redrawn from Vijverberg *et al.* 2009.
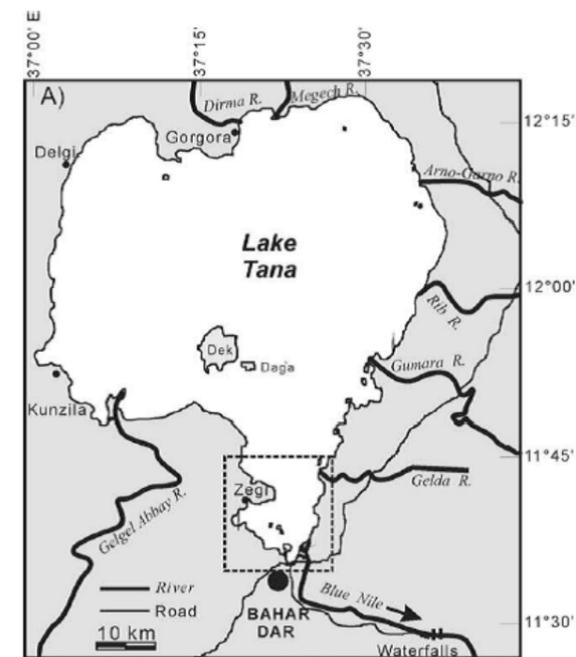
Fig. 2. Lake Tana and its main inflowing rivers. The Blue Nile is the only outflowing river. The dotted right angle shows the Bahar Dar Gulf, the main area of research.
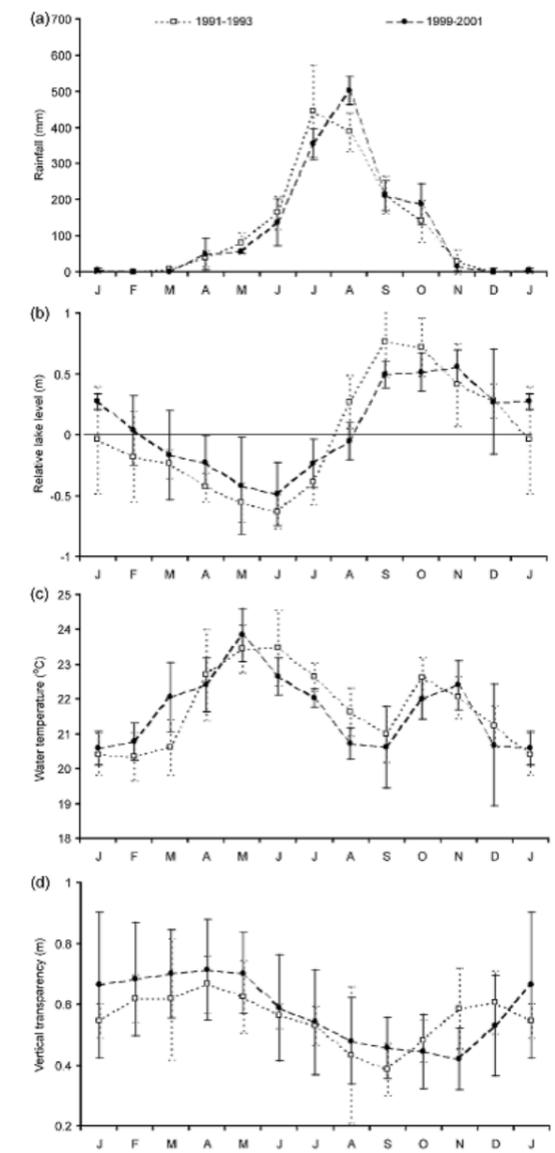
Fig. 3. Monthly changes (mean SE) in (a) rainfall, (b) lake water level, (c) water temperature, and (d) vertical transparency (Secchi depth) in the Bahar Dar Gulf during 1991/1993 (dotted lines, open squares) and 1999/2001 (dotted lines, solid circles). Redrawn from de Graaf *et al.* 2004.

Table 1. Differences in seasonal [s] and inter-annual [a] Relative Lake Level Fluctuations (RLLF) among several African lakes. S = surface, D = mean depth, FT = flushing time, ΔWL = mean change in water level (m); RLLF[s]or[a] = ΔWL [s] or[a] / mean depth * 100 (data Lake Tana (1980-2001) from Wudneh (1998) and references therein, Nagelkerke & Sibbing 1996, Fig. 3b and National Meteorology Office, National Water Resources Department, Addis Ababa, Ethiopia; data other African lakes from Jul-Larssen *et al.* 2003 and references therein). Adapted from de Graaf *et al.* 2004.

| | S | D | FT | Water Level Change (m) | | Relative Lake Level Fluctuation | | Lake Characteristics | |
| | | | | Seasonal | Inter-annual | Seasonal | Inter-annual | Seasonal | Inter-annual |
	(km²)	(m)	(yrs)	ΔWL [s]	ΔWL [a]	RLLF[s]	RLLF[a]	Pulse	Stability
Tana	3100	8	6	1.44	0.08	18.00	1.00	+	+
Tangayika	32600	580	7000	0.78	0.22	0.14	0.04	--	++
Malawi	28800	290	750	0.97	0.28	0.30	0.10	-	+
Victoria	68800	40	140	0.44	0.22	1.10	0.60	-	+
Chilwa	680	3	-	1.19	0.53	39.70	17.80	++	--
Bangweulu	2733	3.5	-	1.20	0.26	34.30	7.40	++	-
Mweru	4650	8	4	2.05	0.58	25.70	7.20	+	-

mortality; and d) high inter-annual variability in biomass (Jul-Larsen *et al.* 2003 and references therein). In Lake Tana, however, the variation of the annual influx of nutrients was low from year to year between 1980-2001 [(low RLLF[a]), Table 1] and the timing was highly predictable, lake levels always peaked in September-October. Lake Tana can therefore be considered, at least for the period under consideration, as a stable environment despite the fact that nutrient influx is externally driven. On the African continent, Lake Tanganyika, Lake Malawi and Lake Victoria are examples of stable systems. Biological production in these large, deep lakes is largely driven by an internal supply of nutrients through vertical mixing. The fish faunas of lakes with constant abiotic conditions and internal energy pathways are characterised by: a) a high biodiversity, b) ecologically specialised endemics with *K*-selected life histories, and c) stable and predictable natural mortality. Lake Tana's *Labeobarbus* species flock are an endemic and ecologically specialised group of fish characteristic of stable systems like the endemic cichlid species flocks of Lake Victoria, Lake Tanganyika and Lake Malawi (Sibbing & Nagelkerke, 2001; Jul-Larsen *et al.* 2003; de Graaf *et al.* 2008). Generalised implications for fisheries exploiting ecologically specialised fish, are

that these fish populations have a low regenerative capacity, a high susceptibility to increased fishing mortality but low inter-annual natural variability in biomass and hence catches (Jul-Larsen *et al.* 2003 and references therein).

2. ICHTHYOFAUNA

Four fish families occur in Lake Tana. The Cichlidae, Clariidae and Balitoridae are represented by only one species each, *Oreochromis niloticus* Linnaeus 1758, *Clarias gariepinus* Burchell 1822 and *Afronemacheilus abyssinicus* Boulenger 1902, respectively. In contrast to the headwater lakes of the White Nile where haplochromine cichlids dominate, the fish fauna of Lake Tana is dominated by the cyprinid fishes represented by four genera, i.e. '*Barbus*', *Garra*, *Labeobarbus* and *Varicorhinus* (one species *V. beso* Rüppell 1836).

'*Barbus*'

Three species of small (< 10 cm) barbs are known from Lake Tana: '*Barbus*' *humilis* Boulenger 1911, '*Barbus*' *pleurogramma* Boulenger 1911 and the recently described pelagic '*Barbus*' *tanapelagius* de Graaf *et al.* 2000. Molecular analyses show the

genetic similarity between the benthivorous *Barbus humilis* and the zooplanktivorous *Barbus tanapelagius*, which presumably evolved from the former species (de Graaf *et al.* 2007).

Garra

According to Boulenger (1911), the genus *Garra* has two species in Lake Tana, *G. dembeensis* Rüppell 1835 and *G. quadrimaculatus* Rüppell 1835. In a recent revision by Stiassny & Getahun (2007) the latter species was re-identified and described as *G. dembecha*, a new species that also occurs outside the lake in Eritrea, Kenya and Tanzania. Stiassny & Getahun (2007) described two additional new endemic species for Lake Tana, viz. *G. regressus* (formerly *G. microstoma;* Getahun 2000) and *G. tana*.

Labeobarbus species flock

The family Cyprinidae is the most widespread and has the highest diversity (> 2400 species; Nelson 2006) among all fresh water fish families and even among vertebrates. Despite the overwhelming abundance of cyprinid fishes throughout the world's fresh water systems, the *Labeobarbus* species of Lake Tana form, as far as we know, the only remaining intact species flock of large cyprinid fishes (Nagelkerke *et al.* 1994), since the one in Lake Lanao in the Philippines, has practically disappeared due to anthropogenic activities (Kornfield & Carpenter 1984). Lake Tana and its *Labeobarbus* species flock provide an unique opportunity to study the selective forces driving speciation, because this species flock is: a) undamaged; b) evolved in a geographically isolated system; and c) small (15

Fig. 4. Heads of the 15 *Labeobarbus* species of Lake Tana.

species) so all species can be studied at the same time. Following detailed studies of morphological and ecological characters (Nagelkerke *et al.* 1994; Nagelkerke & Sibbing, 1997), immuno-genetics (Dixon *et al.* 1996), reproductive segregation (Nagelkerke & Sibbing, 1996) and ontogenetic development (Nagelkerke *et al.* 1995a), the large (up to 100 cm) labeobarbs of Lake Tana were upgraded from distinct morphotypes (Nagelkerke *et al.* 1994) into 15 endemic species in addition to the non-endemic *B. intermedius* (Nagelkerke & Sibbing, 1997, 2000). Although Mina *et al.* (1996) and Dgebuadze *et al.* (1999) only partly agreed on the specific status of the large barbs and favoured the description of the labeobarb diversity by plastic phenotypes of *Barbus intermedius*, several follow-up studies confirmed morphological, ecological, reproductive and genetic segregation (Kruiswijk *et al.* 2005; de Graaf *et al.* 2008; de Graaf *et al.* 2010a,b,c; Palstra *et al.* 2004; de Graaf *et al.* 2005). The genus *Labeobarbus* is assigned to Lake Tana's large hexaploid (Golubtsov & Krysanov, 1993) cyprinids following suggestions by Bini (1940), Berrebi (1995), Nagelkerke & Sibbing (2000), Skelton (2001, 2002) and Berrebi & Tsigenopoulos (2003). This better reflects their phylogenetic distance to other members of the overly 'lumped' genus '*Barbus*' (Tsigenopoulos *et al.* 2002) including the small diploid barbs of Lake Tana (de Graaf *et al.* 2007; de Graaf *et al.* 2010a).

Based on resource use along trophic, spatial and temporal dimensions, an ecological 'tree' for the Lake Tana cyprinid species flock was developed by de Graaf *et al.* (2008) (Fig. 5) reflecting the evolutionary hypothesis for adaptive radiation. In general, ecological segregation is most pronounced along the spatial dimension dividing the species flock into several macro-habitats followed by trophic segregation (diet and predation technique) within each habitat assemblage. Morphological (body colouration) and behavioural (reproductive strategy) adaptations to macro-habitat appear clearly present in Lake Tana's inshore and offshore clades (Fig. 5). The sexually monomorphic *Labeobarbus* belonging to the inshore clade are lacustrine spawners with darker body colouration and narrow distribution patterns. This sharply contrasts to the riverine spawning offshore clade of sexually monomorphic *Labeobarbus* species that are widely distributed, occurring throughout the sub-littoral and offshore waters and have a silvery white body.

The secondary radiation involves trophic structures, specializing the feeding apparatus (head morphol-
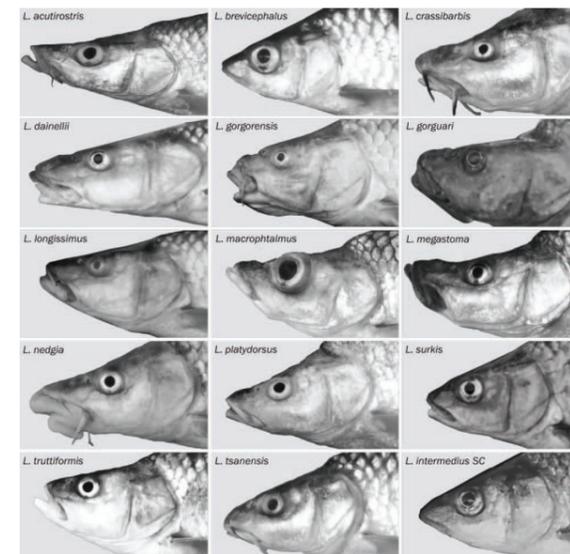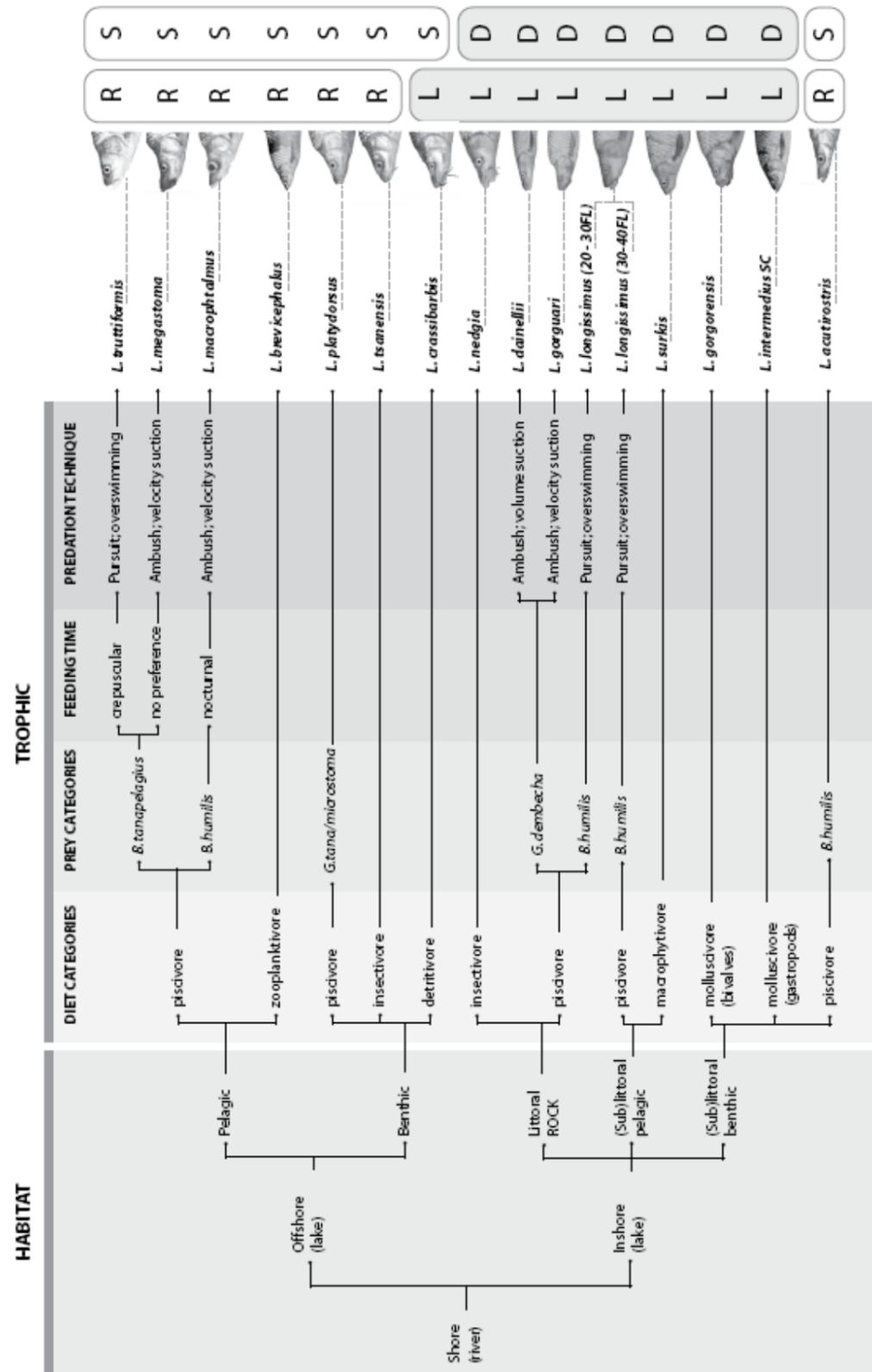
Fig. 5. A schematic ecological tree illustrating the hypothesised sequential waves of radiation in the evolution of the *Labeobarbus* species flock of Lake Tana (predation techniques [de Graaf 2003]: reproductive strategies; R = riverine spawners, ancestral strategy, L = lacustrine spawners, derived strategy [de Graaf *et al.* 2005; Palstra *et al.* 2004]); body colouration S = silvery, D = dark. Note that reproductive strategy and body colouration of the labeobarbs are strongly associated with habitat. Redrawn from de Graaf *et al.* 2008.

Table 2. Overview of freshwater fishery statistics of water bodies in the Nile catchement after the 1990s. Egypt: Khalil 1997; Feidi 2001; Dumont & El-Shabrawy 2007. Sudan: AI El-Moghraby unpublished; Coenen, 1991; East African Lakes NaFIRRI CAS Reports 2006 & 2007; LVFO CAS Reports 2006 & 2007. Lake Tana: Wudneh 1998; de Graaf *et al.* 2006; de Graaf personal communications with fishermen and staff Bureau of Agriculture and Rural Development, Bahar Dar, February 2010. Redrawn from Witte *et al.* 2009.

Area	Surface (km²)	Fish landings (t y⁻¹)	Year	Main fish taxa	Production (t y⁻¹ km²)	Fisher density (no/km²)
Egypt						
Lake Borullus	460	50,000	1990-2004	Tilapiine cichlids, *Clarias*	108.7	
Lake Manzala	840	55,000	1989-1993	Tilapiine cichlids	65.4	
Lake Nasser	6,000	41,000	1999	*Oreochomis,* Cyprinids	6.8	0.5
Sudan						
Lake Nubia	1140	1000	2003		0.9	
Gebel Aulia Res.	1500	13 000	2003		8.7	
Sennar Res.	160	1000	2003		6.3	
Roseires Res	290	1500	2003		5.2	
Sudd	35,000	30 000	2003		0.9	
East African Lakes						
Lake Albert	6,800	182 000	2007	*Brycinus, Neobola; Lates, Bagrus*	26.8	1.7
Lake Edward/ George	2,600	11,000	1991	*Oreochromis, Protopterus, Clarias,* haplochromines	4.2	2.5
Lake Kyoga	2,700	34 700	2006	*Rastrineobola, Oreochromis, Lates, Protopterus*	12.9	2.2
Lake Victoria	68 800	1 000 000		*Rastrineobola, Lates, Oreochromis,* haplochromines	14.5	0.4
Ethiopia						
Lake Tana	3,100	1000	1987-2001	*Oreochromis, Labeobarbus, Clarias*	0.3	0.15
	3500		*2010*		*1.1*	*0.55*

ogy, Fig. 4). Lake Tana's *Labeobarbus* species have evolved unique anatomical features adapting them to specific food types (Sibbing et al, 1998; Sibbing & Nagelkerke 2001). In our evolutionary scenario, trophic specializations like piscivory have separate, independent origins within the species flock. A sequence of macro-habitat diversification, followed by trophic diversification within each macro-habitat has been reported for lacustrine East African cichlids (Seehausen 1996; Sturmbauer 1998; Rüber *et al.* 1999; Danley & Kocher 2001), arctic charr (Snorrason *et al.* 1989), anoline lizards and Darwin's finches (Streelman & Danley 2003). Diversification according to sexual selection models (female mate choice) as a driving force for speciation among the ecologically diverse, monomorphic labeobarbs of Lake Tana seems unlikely at this stage of their evolution. Future research should focus on resolving the phylogeny of Lake Tana's species flock to test if our hypothesized evolutionary scenario (de Graaf *et al.* 2008), i.e. sequential episodes of diversification and the replicated evolution of trophic specializations in different habitats, is corroborated by molecular data.

3. EXPLOITATION OF LAKE TANA'S FISH RESOURCES

Fishing has never been an important activity in Ethiopian history. Fish is not highly valued as a source of cheap protein and is mainly eaten during religious fasting periods. On average, an Ethiopian eats only 0.1 kg of fish per year. However, the distribution of fish consumption is highly skewed towards the shore areas of lakes (8-10 kg yr^{-1}) and also to the capital city Addis Ababa (1 kg yr^{-1}). To maximise their income, the fishermen specifically target *O. niloticus,* the most favoured fish for consumption among Ethiopians. *Labeobarbus* is less appreciated due to its intramuscular bones and is therefore mainly used for soup or 'wot', a spicy (chopped) fish sauce. The scale-less *C. gariepinus* is considered unclean according to the Ethiopian Orthodox Church and is almost exclusively eaten by Western and African foreigners in Addis Ababa. Unlike practice at other African lakes, Lake Tana's small sized (< 10 cm) fish species, like the pelagic zooplanktivore *Barbus tanapelagius*, are at present not harvested (Dejen *et al.* 2009).
Compared to other water bodies in the Nile Basin (Table 2) fish production and fisher density in Lake Tana are low. This is likely partly due to the oligo-

mesotrophic nature and low water transparency (0.4-0.7 m, Fig. 3) of this high altitude lake. Lake Tana's gross primary production rates were among the lowest compared with 25 other tropical lakes (Wondie *et al.* 2007; Dejen *et al.* 2009), while underutilization of Lake Tana's fish resources has also been suggested (Wudneh 1998). Unfortunately, since 2001 little reliable data on the development of the fish stocks, traditional fisheries and modern fisheries have been collected. This is regrettable, especially if the reports of a sharp increase during the last 10 years of modern motorised boats from 5 to 50-100 and traditional reed boats from 400 to 1600 is true (de Graaf, personal communications with fishermen and staff from the Bureau of Agriculture and Rural Development, February 2010).

Lake Tana's fisheries

Before 1986 Lake Tana fisheries was composed of two predominantly subsistence traditional fisheries. The first is a reed boat fishery, operated by the Woito people (ethnic minority). This type of fishery is limited to the shore areas and targets the native *Oreochromis niloticus*, using locally made fish traps and small gillnets (length 15-20 m). Secondly, seasonal fishermen (farmers) traditionally target *Labeobarbus* on the upstream spawning grounds between August and October each year (Fig. 7a). These seasonal fishermen use a variety of fishing techniques like barriers, basket traps, hooks, scoop nets and even poisoning of the shallow water upstream using the dried and crushed seeds of the berberra tree (*Milletia ferruginea*, Leguminosae; Nagelkerke and Sibbing 1996). This seasonal fishery has been occurring for at least 200 years, and most probably for hundreds of years more, as fishing with poison was already observed and described around 1770 by the Scottish explorer James Bruce during his travels around Lake Tana (p. 36; Moorehead 1962).
Motorised boats and modern, more efficient, nylon gillnets were introduced in Lake Tana in 1986, to fulfil the increasing demand for fish from Addis Ababa (Reyntjes *et al.* 1998), largely created by foreigners. The development of commercial motorised gillnet fishery in Lake Tana has benefited considerably from assistance by Dutch NGOs and the EU sponsored Lake Fisheries Development Program. In the late 1980s the new motorised gillnet fleet consisted of ~ 20 boats and was manned by a new group of ~100 inexperienced Amhara fishermen (ethnic majority).

After the initial investments in Lake Tana's motorized gill net fisheries at the end of the 1980s, the number of operating boats (maximum 23) started to decrease due to mechanical failure and lack of spare parts. In 2003 a Dutch NGO donated five new fishing boats and a new collection boat to the fishermen in the small town of Zegi in the Bahar Dar Gulf.
The whole catch of reed boat fishermen and seasonal river fishermen is sold on local markets and to restaurants around Lake Tana. In contrast, almost all fish landed by the motorised gillnet fishery is transported to Addis Ababa. Only in recent years has the export of dried fish from Lake Tana to neighbouring Sudan started up.

Changes in Lake Tana's fish stocks and fisheries 1991-2001 and 2001-2010

During a census in the early 1990s 113 reed boat fishermen (one per boat) were counted in the Bahar Dar Gulf, fishing with a total of 374 gill nets of on average 18 m length, 8 cm stretched mesh (Wudneh 1998). The overall mean catch per unit of effort (CPUE in kg per day) for the reed boats was 12.3 kg (7.8 kg *O. niloticus*, 4.3 kg *Labeobarbu*s spp and 0.2 kg *Clarias gariepinus*; Wudneh 1998 Fig. 6). Between 1991 and 2001 the CPUE of labeobarbs decreased sharply from 4 to 0.3 kg per fishing trip while the CPUE for *O. niloticus* and *C. gariepinus* remained largely unchanged (Fig. 6). Between 1991 and 2001 the total number of reed boat fishermen in the lake has been assumed to remain stable at around 400, landing around 800 t of fish annually. However, during discussions with staff of the Bureau of Agriculture and Rural Development in February 2010 it became apparent that the number of reed boat fishermen may need to be corrected. Unofficial results of a census conducted in 2009 appear to indicate that the number of reed boat fishermen may be as high as 1500. While previously the catch of the reed boat fishery was sold at the local markets around Lake Tana, at present, part of the catch is dried and sold to neighbouring Sudan.
Ameha and Assefa (2002) reported that the amount of fish caught on the spawning grounds of the Gumara River by seasonal fishermen fluctuated between 2.5 and 25 t (Fig. 7b) during the 1990s. It is, unfortunately, unclear if these fluctuations in fish are due to differences in fishing effort by the seasonal fishermen or represent actual changes in the size of the spawning populations. In Lake Victoria a similar traditional

fishery targeting large cyprinid fishes, using barriers and basket traps along the rivers, appeared to have little deleterious effect on *Labeo* and (*Labeo*)*barbus* stocks (Ogutu-Ohwayo 1990). The introduction of more efficient gill nets at the mouths of the rivers during the spawning period, on the other hand, did damage the sustainability of this fishery (Cadwalladr 1965; Ogutu-Ohwayo 1990). Originally the seasonal fishery during the spawning migration may have been sustainable in Lake Tana's rivers. It is, however, unlikely that with the increase in population numbers in Ethiopia, the seasonal fishery on spawning labeobarbs can be maintained at a sustainable level. The enormous amounts of fishermen concentrated on a small section of the Gelda River, as shown in Fig. 7a, has not been observed for almost 15 years.
A modern fishery with motorised boats and efficient gillnets was introduced relatively late into Lake Tana. In the late 1980s and early 1990s effort, CPUE and total landings increased annually (Fig. 8). Annual yield peaked in 1993 (388 t yr^{-1}) but gradually decreased until 2003 (lowest catch in 2000 [139 t yr^{-1}]). Number of gillnets (20 per boats), mesh size (10 cm stretched mesh) and number of fishing days per month (20) did not change during the 1990s (de Graaf *et al.* 2006). Since 2003 (148 t yr^{-1}) total catch has increased again resulting in a doubling of the catch in 2006 (292 t yr^{-1}). Until at least 2001, the vast majority of the catch by the motorised gillnet fishery was sold to the only fish buyer (Fish Production and Marketing Enterprise) and until 2011 the catch figures in Fig. 8 most likely represent the total catch of the commercial gillnet fishery for the whole of Lake Tana. Recent discussions with fishermen (February 2010) and preliminary results of the 2009 fisher census made it clear that between 2001 and 2010 major changes have occurred in the motorised gillnet fishery. In recent years the number of fish buyers has increased (~5-10) and the number of boats may have increased from 5-10 to between 50 and 100. In the past Lake Tana fishermen depended on foreign NGOs to get steel boats. This is no longer the case, as steel boats are currently manufactured in Bahar Dar on demand. During the 1990s significant changes occurred in effort allocation, species composition and abundance of fish stocks. In 1991-1993 the vast majority (70%) of fishing activity took place in the Bahar Dar Gulf and only 15% of the effort was allocated to the northeastern shores of the lake. After 1991-1993 the gillnet fishery moved in a northern direction. In 2001 40%
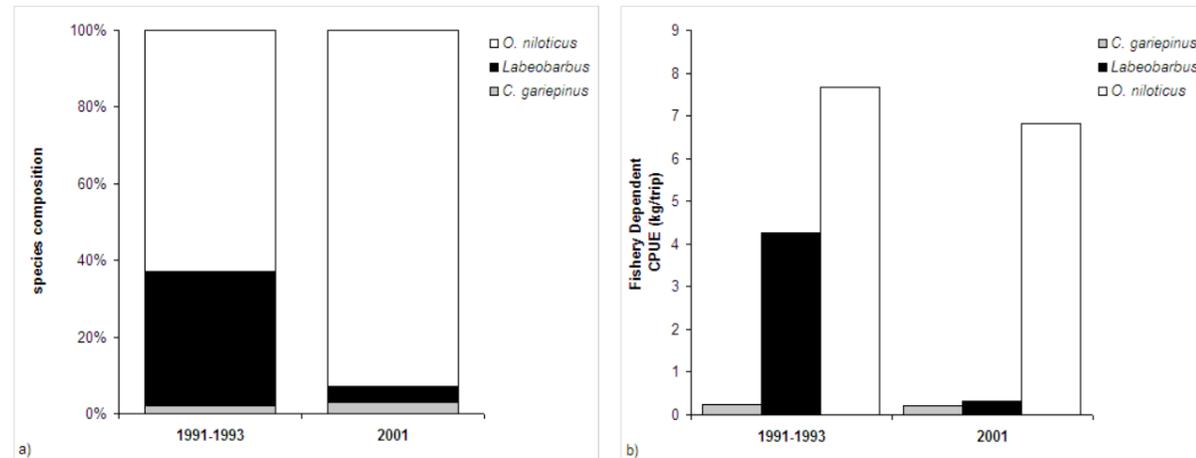
Fig. 6. Changes in the species composition (a) and CPUE of the reed boat fishery between the early 1990s and 2001 (data 1991-1993 from Wudneh 1998; data 2001 de Graaf unpublished results.
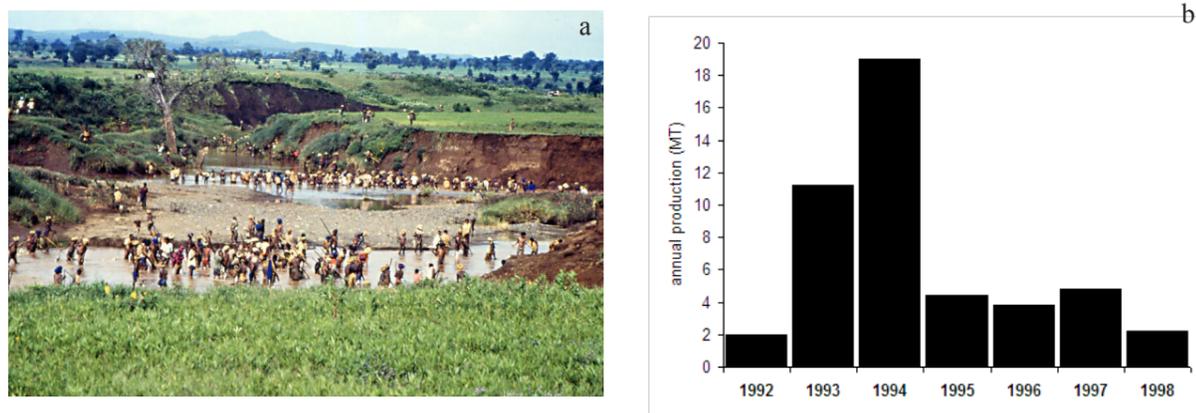
Fig.7. a) Hundreds of seasonal fishermen targeting the migratory labeobarbs in the Gelda River in the early 1990 (Nagelkerke & Sibbing 1996). b) Total catch of *Labeobarbus* species of the seasonal fishery in Gumare River. Redrawn from Ameha and Assefa 2002
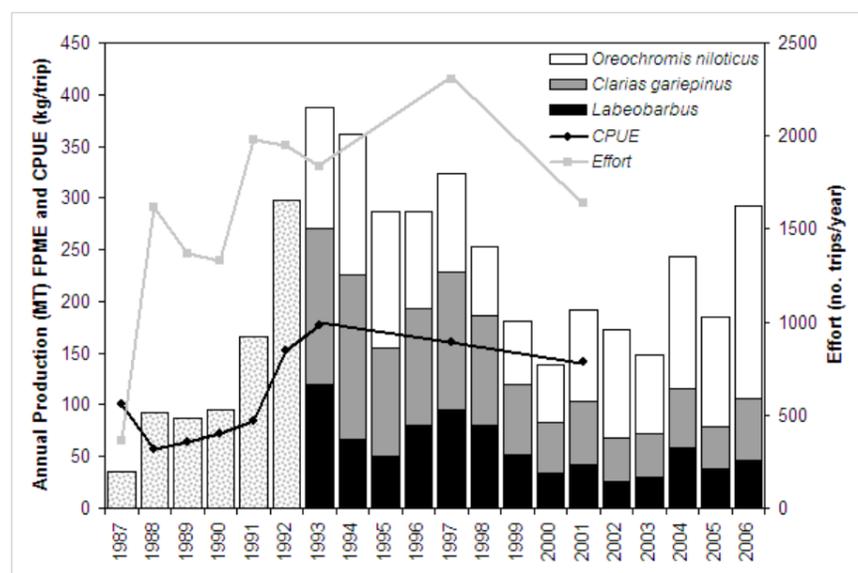
Fig. 8. Estimated total annual yield (bars, tonnes/year), total effort (grey solid squares, trips/year) and total CPUE (solid circles, kg/trip) of the motorised gill net fishery in Lake Tana. Redrawn from de Graaf *et al*. (2006). Data on annual catch from Fish Production and Marketing Enterprise. Note that the species composition of the annual catch data 1987-1993 is unknown.

of the effort was allocated to the north-eastern shores of Lake Tana adjacent to the floodplains. During the 1990s *Oreochromis niloticus*, *Clarias gariepinus* and *Labeobarbus* each made up roughly a third of the total catch; however, since 2001 the contribution of *O. niloticus* had doubled to more than 50%, while the contribution of both *C. gariepinus* and *Labeobarbus* halved (Fig. 8). CPUE of *O. niloticus* almost doubled during the 1990s, without affecting the abundance of tilapia as determined by fishery-independent trawl surveys (Fig. 9). In contrast CPUE and abundance of *Labeobarbus* decreased by 50% and 75%, respectively during this period (Fig. 9). Preliminary results of the 2010-2011 fisheries monitoring program appear to demonstrate a further drastic decline of the *Labeobarbus* stocks. Between 2000 and 2010 CPUE (kg of fish per day per boat) decreased from ~30 kg to less than ~10 kg per day in 2011.

Future of Lake Tana's fish and fisheries
In Lake Tana, the relatively unspecialised ecologically flexible species such as *O. niloticus* and *C. gariepinus*, which are adapted to fluctuating environments, can be categorised as resilient (Table 3). The increase in fishing efforts after the introduction of the motorised commercial gillnet fishery has had a mod-

erate effect on both species between 1991 and 2001 in comparison with the decline of the labeobarbs (de Graaf *et al*. 2006). A reduction of larger and older specimens as shown in Fig. 10 was to be expected with an increase in fishing effort. However, the number of juveniles has remained similar during this period (Fig. 10).

In sharp contrast to *Oreochromis niloticus* and *Clarias gariepinus*, the *Labeobarbus* species are predicted to be by far the most susceptible to fisheries as the labeobarbs are: (a) long-lived (Wudneh 1998),
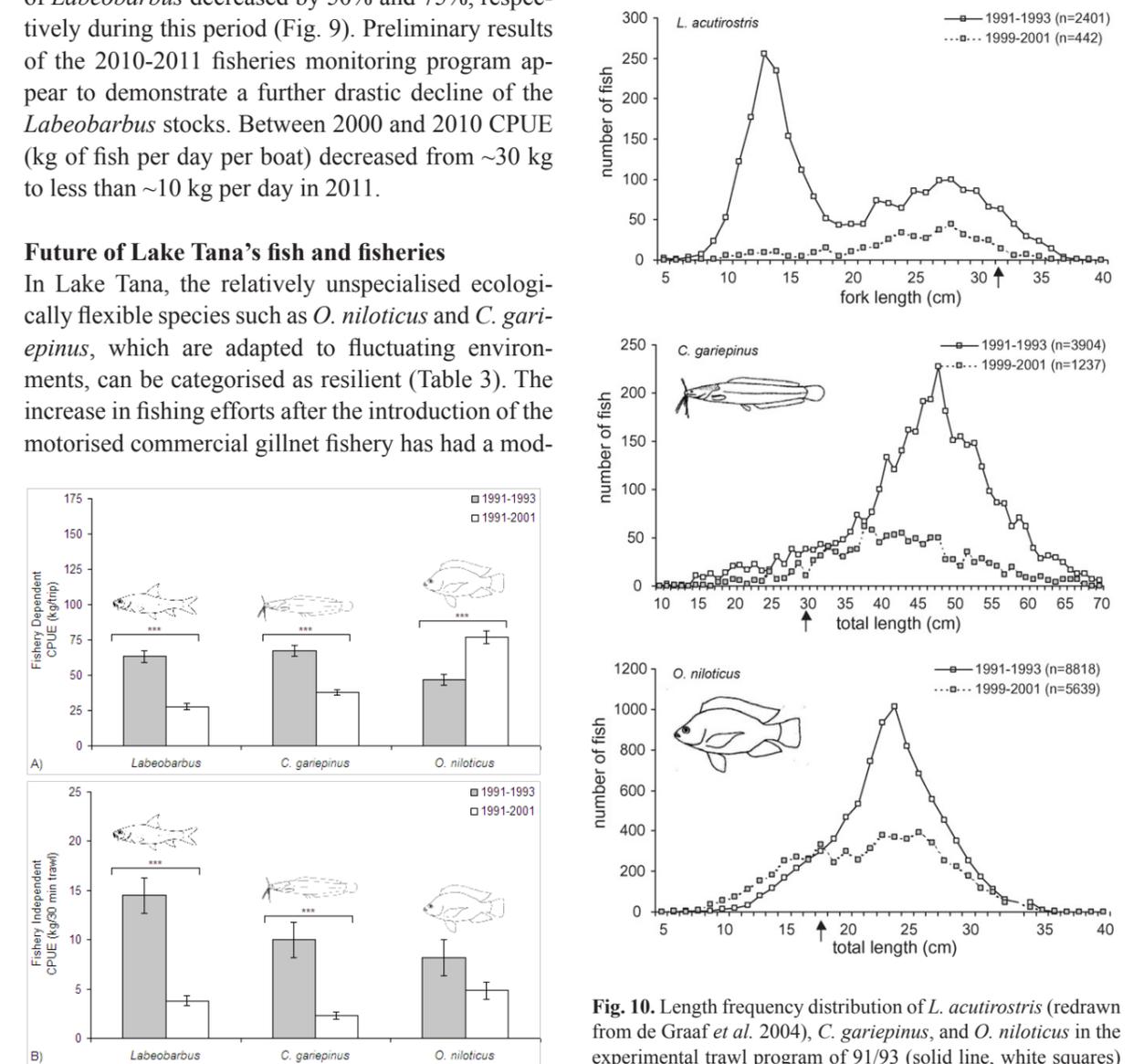
Fig. 9. Temporal variation in (a) CPUE of the commercial gillnet fishery and (b) the experimental trawl surveys (b) in *Labeobarbus*, *C. gariepinus* and *O. niloticus* during 1991-1993 and 1999-2001 (redrawn from de Graaf *et al*. 2006). Error bars indicate 95% confidence interval; *** = P< 0.001.
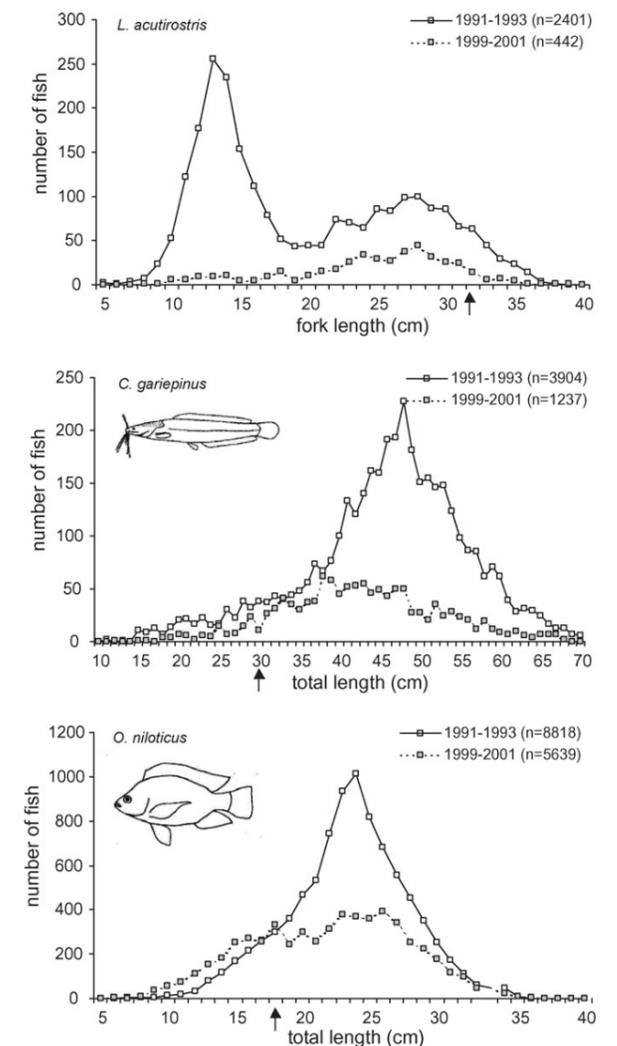
Fig. 10. Length frequency distribution of *L. acutirostris* (redrawn from de Graaf *et al*. 2004), *C. gariepinus*, and *O. niloticus* in the experimental trawl program of 91/93 (solid line, white squares) and of 99/01 (dotted line, grey squares). (see also Table 3). Note the collapse of juvenile *L. acutirostris* in the period 1999-2001, the decline of large *C. gariepinus* (> 40 cm TL) and *O. niloticus* (> 20 cm TL), and the increase of small *O. niloticus* (< 20 cm TL) between the two periods. Arrows indicate female size at maturity (FL50%); data *L. acutirostris* (99-01 de Graaf *et al*. 2003), *C. gariepinus* and *O. niloticus* (91-93 Wudneh, 1998).

Table 3. Aspects of general biology and predicted susceptibility to fishery in Lake Tana of adult *Labeobarbus, C. gariepinus* and *O. niloticus*. References (Ref.): 1 = de Graaf *et al.* 2005; 2 = Wudneh 1998; 3 = this paper; 4 = Palstra *et al.* 2004; 5 = Witte and van Densen 1995; 6 = Winemiller & Kelso-Winemiller 1994; 7 = Twongo 1995; 8 = de Graaf 2003; 9 = Sibbing & Nagelkerke 2001; 10 = Goudswaard *et al.* 2002; 11 = Duponchelle & Panfili 1998; 12 = Kolding 1993.

	Labeobarbus species flock	*Clarias gariepinus*	*Oreochromis niloticus*	Ref.
Reproductive biology				
Spawning period	2 months, August-September	2 months, June-July	throughout the year	1, 2
Spawning aggregation & migration	spawning aggregations in river mouths of major affluent rivers	migration from sublittoral/bentho-pelagic towards littoral areas and floodplains during inundation	migration from littoral zone into floodplains during inundation	1, 2, 3
Spawning area	Riverine spawners: upstream areas major affluent rivers Lacustrine spawners: littoral zones, floodplains?	Floodplains, wide habitat tolerance for spawning and nursery areas	Floodplains, wide habitat tolerance for spawning and nursery areas	1, 4, 5, 6, 7
Age at maturity	3-5 years	2-3 years	1-2 years, highly flexible	2, 11, 12
Ecology				
Diet	Narrow, mostly food specialists	Broad, omnivore	Intermediate, planktivore (opportunist)	5, 6, 8, 9, 10
	piscivore, benthivore, macrophytivore, molluscivore, insect-zooplanktivore	fish, insects, plankton, plants, molluscs, detritus	phyto-, zooplankton, diatoms, detritus, molluscs, insect larvae	
Habitat	riverine spawners: sublittoral/pelagic, bottom and surface lacustrine spawners: littoral zone	sublittoral/bentho-pelagic zone, bottom dwelling	littoral zone bordering floodplains	2, 3, 8
Susceptibility to fishery	High Vulnerable	Moderate Resilient	Low Most resilient	

(b) form spawning aggregations (Nagelkerke and Sibbing 1996; Palstra *et al.* 2004; de Graaf *et al.* 2005), and (c) are predominantly ecologically highly specialised endemics (Sibbing and Nagelkerke 2001; de Graaf *et al.* 2008). A drastic decrease in abundance by ca. 75% of the migratory riverine spawning *Labeobarbus* species and the collapse of juvenile *Labeobarbus* (as illustrated by a 90% reduction of juvenile (5-18 cm FL) *L. acutirostris* between; Fig. 10) during the 1990s suggest recruitment-overfishing (de Graaf *et al.* 2004; de Graaf *et al.* 2006). The most likely cause for the dramatic decline in *Labeobarbus* stocks is the introduction of the motorised commercial gillnet fishery as no changes were recorded in the traditional fisheries (de Graaf *et al.* 2006) and the lake's environment (de Graaf *et al.* 2004). *Labeobarbus* catchability is highly variable during the year (Fig. 11), more than 50% of the annual *Labeobarbus* yield is landed during the three month of peak spawning, July-September, when fishermen target the spawning aggregations in the river mouths. In de Graaf *et al.* (2004 and 2006) riverine and lacustrine species were not analysed separately. The experimental trawl data will need to be reanalysed in the near future to determine whether both riverine and lacustrine species have declined or only riverine species.

The drastic and rapid consequences of an unregulated gillnet fishery on spawning aggregations of large African cyprinid fishes has become painfully clear with the collapses of *Labeo mesops* fisheries in Lake Malawi (Skelton *et al.* 1991), *Labeo victorianus* and *Barbus altianalis* fisheries in Lake Victoria (Cadwalladr 1965; Ogutu-Ohwayo 1990; Ochumba and Manyala 1992) and the virtual disappearance of *Labeo altivelis* from the Mweru-Luapula system within a period of 20 years (Gordon 2003).

The situation of the unique *Labeobarbus* species flock is critical. Nagelkerke *et al.* (1995b) already warned against fisheries at the river mouths entering Lake Tana. To remove the threat of extinction for Lake Tana's endemic *Labeobarbus*, effort control regulations limiting the gillnet and reed boat fishery in the spawning season and/or areas around the river mouths and seasonal fishery on the upstream spawning areas are to be implemented immediately to prevent a total collapse of the *Labeobarbus* species dependent on riverine spawning. Erosion of river banks, due to poor land management practises, causes further pressure on the reproductive success of riverine spawning labeobarbs. The removal of natural vegetation (shrubs and trees) along the river banks and the use of land right up to the river bank for agriculture purposes have led to increased erosion and sedimentation. The sedimentation load could have detrimental consequences for developing fish larvae and eggs as riverine spawning labeobarbs require clear, fast flowing, highly oxygenated streams with rocky substrate to successfully reproduce. Unfortunately the changes in sedimentation load and possible impact on the reproductive success has not been quantified. However, poor land use could possibly be an alternative explanation for the strong decline of riverine *Labeobarbus* species since the 1990s.

A possible final blow to the survival of riverine spawning *Labeobarbus* species are the planned irrigation dams in Ribb, Gumara and Megech Rivers (Alemayehu *et al.* 2009) and the expected negative effects on Lake Tana's water level of the Tana-Beles hydropower station. The location of the irrigation dam that is currently being constructed in the Ribb River is in the middle of the spawning grounds. An irrigation dam (Getahun *et al.* 2008) will cause: a) the loss of spawning habitats upstream from the dam; b) reduced flow over the dam during the spawning season which will prevent sufficient inundation of spawning areas downstream from the dam, preventing successful reproduction; and c) reduced flow over the dam which will prevent the sufficient inundation of flood plains near the river mouth, negatively affecting fish
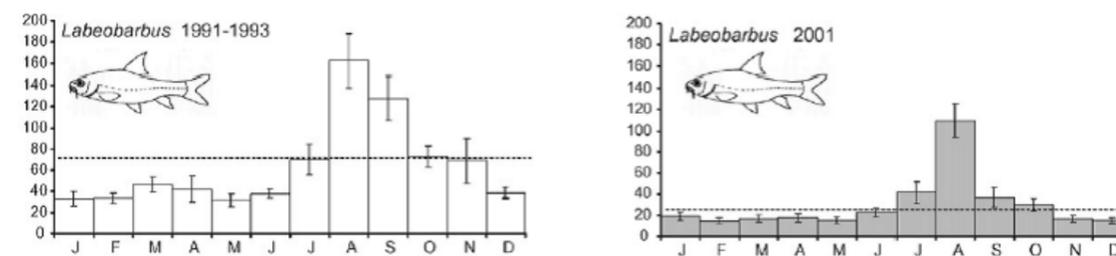
Fig. 11. Temporal variation in *Labeobarbus* CPUE of the commercial gillnet fishery during 1991-1993 and 2001. Dotted lines indicate overall mean, error bars indicate 95% confidence intervals. Redrawn from de Graaf *et al.* 2006.

(also including *O. niloticus* nursery grounds) and farmers. The Chara Chara weir in the outflow of the Blue Nile has had a significant effect on the water level and water flow out of the lake (McCartney *et al.* 2010). Since the weir became fully operational in 2001, the seasonal flow has been almost completely dampened. If all the planned water developments are implemented Lake Tana's water level is expected to drop by more than 0.5 m (McCartney *et al.* 2010).

In the past no management plan has been developed due to the: (a) the lack of a federal fisheries legislation; (b) the lack of data on the characteristics of both the fish stocks spawning period, and of the commercial gillnet fishery; and (c) the lack of knowledge dissemination, i.e. the relevant information is published in English in international scientific journals, hence less accessible for local experts, civil servants and policy makers. Recently (January 2003) Ethiopia's first fisheries legislation was approved by the federal government. The next step is an adequate control system to enforce the regulations. To make the most of this positive development and in co-operation with the Amhara Region Agricultural Research Institute, several activities have been implemented to disseminate the wealth of knowledge on Lake Tana's fish and fisheries that has been generated in recent years. In November 2003 the first national workshop on Ethiopian fish and fisheries was organised in Bahar Dar to develop management and research strategies with the participation of policy makers, researchers and private stakeholders. In 2006 a book was published in the local Amharic language, containing basic data on the fish stocks and fisheries collected in the last decade and the research and management strategies formulated at the workshop. In May 2007 the Ethiopian Fisheries and Aquatic Sciences Association was established under the main objective to develop the sustainable exploitation of aquatic resources and conservation of fish and other aquatic biota.

For the conservation of the Lake Tana ecosystem, continuous monitoring of the catches of traditional and modern fisheries and conducting regular fishery-independent sampling programs are of utmost importance to on one hand determine the condition of the stocks and on the other to evaluate the consequences of implemented regulations and potentially devastating developments like the construction of irrigation dams in spawning rivers. An integrated management plan for the Lake Tana basin is urgently required to prevent the collapse of an important fishery and the extinction of the only known cyprinid species flock in the world.

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The Fish Fauna of Lake Victoria during a Century of Human Induced Perturbations

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ABSTRACT

Witte, F., Kishe-Machumu, M. A., Mkumbo, O. C., Wanink, J. H., Goudswaard, P. C., Van Rijssel, J.C. & van Oijen, M. J.P. The fish fauna of Lake Victoria during a century of human induced perturbations. In J. Snoeks & A. Getahun (eds), *Proceedings of the Fourth International Conference on African Fish and Fisheries, Addis Ababa, Ethiopia, 22-26 September 2008.* Tervuren: Royal Museum for Central Africa, 'Zoological Documentation Online Series', pp. 49-66.

Lake Victoria, by area the largest tropical lake of the world, is well-known for its diverse native fish fauna, which comprised about 500 endemic haplochromine cichlid species, two tilapiine species and 46 other species belonging to 12 families. During the past decades, the fish species diversity in the lake has declined dramatically due to human induced perturbations in the ecosystem. Based on literature and our own research findings we provide an overview of these changes and their most likely causes. During the first half of the last century, the increasing fishing pressure had a great impact on the native tilapiine cichlids and other large fish species. The shift in fish landings showed a classic example of fishing down the food web. Because of the dwindling catches, the Nile perch and four exotic tilapiine cichlids were introduced into the lake in the 1950s. Dramatic changes in the fish fauna occurred in the 1980s, with the upsurge of the introduced Nile perch and Nile tilapia, the decline of wetland zones, and increased eutrophication of the lake. The native tilapiines were replaced by the Nile tilapia, and several of the catfish species showed a dramatic decline, as did the lungfish. Most severely hit were the haplochromine cichlids, which disappeared from large parts of the lake, probably resulting in the extinction of many species. The introduced Nile perch and Nile tilapia, and the native cyprinid *Rastrineobola argentea* became the dominant fish species. Though water quality deteriorated and fish diversity decreased, fish landings rose from about 100,000 t y^{-1} in the 1970s to approximately 1 million t y^{-1} in the period 2005-2007. Since 1999 the biomass of Nile perch declined, whereas that of *R. argentea* increased. In the same period some of the sublittoral haplochromine species have recovered. Some of the surviving fish species, show remarkable changes in ecological and morphological features relative to the pre-Nile perch period, which seem to be adaptive responses to the changed environment. Although it may be possible to reconcile fisheries sustainability with biodiversity conservation in the lake basin, measures to reduce environmental stress in the lake are an urgent issue.

Keywords: biodiversity, environmental degradation, eutrophication, extinction, fishery, haplochromine cichlids, Nile perch, speciation, species introductions

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INTRODUCTION

With a surface area of 68,800 km², Lake Victoria is the largest tropical lake in the world. It has a maximum depth of 70 m, which is relatively shallow compared to other large lakes in East Africa (Fryer & Iles 1972). The lake is well known for its high fish species diversity, dominated by haplochromine cichlids (Greenwood 1974; Seehausen 1996; Witte *et al.* 2007a). During the past century, dramatic anthropogenic changes were observed in the lake's ecosystem. Fishery, species introductions and increasing eutrophication had an enormous impact on the fish fauna of the lake (e.g. Ogutu-Ohwayo 1990a; Witte *et al.* 1992; Verschuren *et al.* 2002; Hecky *et al.* 2010). The present paper aims to give a review of the changes in the fish fauna of Lake Victoria and to discuss the potential causes of these changes. For this purpose we roughly divided the history of the lake over the past century into two periods: (1) before and during the 1980s and (2) after the 1980s.

LAKE VICTORIA AND ITS FISH DIVERSITY BEFORE AND DURING THE 1980S

More than 500 endemic haplochromine cichlid species, all maternal mouth brooders, are known from Lake Victoria (Greenwood 1974; Kaufman & Ochumba 1993; Seehausen 1996; Witte *et al.* 2007a). Furthermore, Lake Victoria used to harbour two native tilapiine cichlids, and 46 native non-cichlid species (Table 1), of which 16 are endemic to the lake and its drainage basin (Greenwood 1974; van Oijen 1995). The native non-cichlid species belong to 12 families (Table 1; Fig. 1). In the 1950s, the Nile perch, *Lates niloticus* (Linnaeus, 1758), Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758) and three other tilapiine species were introduced into the lake (Welcomme 1988; Pringle 2005). From the end of the 1960s till the beginning of the 1980s, the haplochromine cichlids made up more than 80% of the demersal fish catches (Fig. 2b; Kudhongania & Cordone 1974). Other prominent species in bottom trawl catches were *Oreochromis esculentus* (Graham, 1929), *O. variabilis* (Boulenger, 1906), *Clarias gariepinus* (Burchell,1822), *Protopterus aethiopicus* Heckel, 1851 and *Bagrus docmak* Forsskål, 1775 (Kudhongania & Cordone 1974; Goudswaard & Witte 1997; Goudswaard *et al.* 2002a, b). Apart from these demersal fishes, the small pelagic cypri-

Table 1. Total number of fish species native to Lake Victoria arranged by family and number of species that were introduced into the lake. Sources: Greenwood 1966, 1974; Kaufman & Ochumba 1993; van Oijen 1995; Seehausen 1996; Witte *et al.* 2007a.

Families/tribes	Number of native species	Introduced species
Protopteridae	1	
Mormyridae	7	
Alestidae	2	
Cyprinidae	17	
Bagridae	1	
Schilbeidae	1	
Clariidae	6	
Mochokidae	2	
Nothobranchiidae	2	
Poeciliidae	5	
Latidae		1
Cichlidae/ haplochromines	ca 500	
Cichlidae/ tilapiines	2	4
Anabantidae	1	
Mastacembelidae	1	

nid *Rastrineobola argentea* (Pellegrin, 1904) made an important contribution to the fish fauna in the lake (Okedi 1974).

Lake Victoria haplochromines have been classified into 15 (sub)trophic groups, each consisting of species sharing morphological characters related to the capture, uptake, and processing of their dominant food source (Greenwood 1974; Witte & van Oijen 1990). The distribution of trophic groups is habitat dependent. For instance, epilithic algae grazers are restricted to rocky shores; insectivores and oral shelling molluscivores are mainly associated with hard substrates like sand and rocks; and detritivores are concentrated near mud bottoms (e.g. Greenwood 1974; Witte 1981; Witte *et al.* 1992; Seehausen *et al.* 1997b).

With respect to the total number of species, the piscivores and insectivores were the most common groups (Fig. 3a), however, the detritivores and zooplanktivores were the most important with respect to biomass, at least in the sub-littoral habitat (6-20 m deep; Fig. 3b), and probably also in the open waters of the lake.
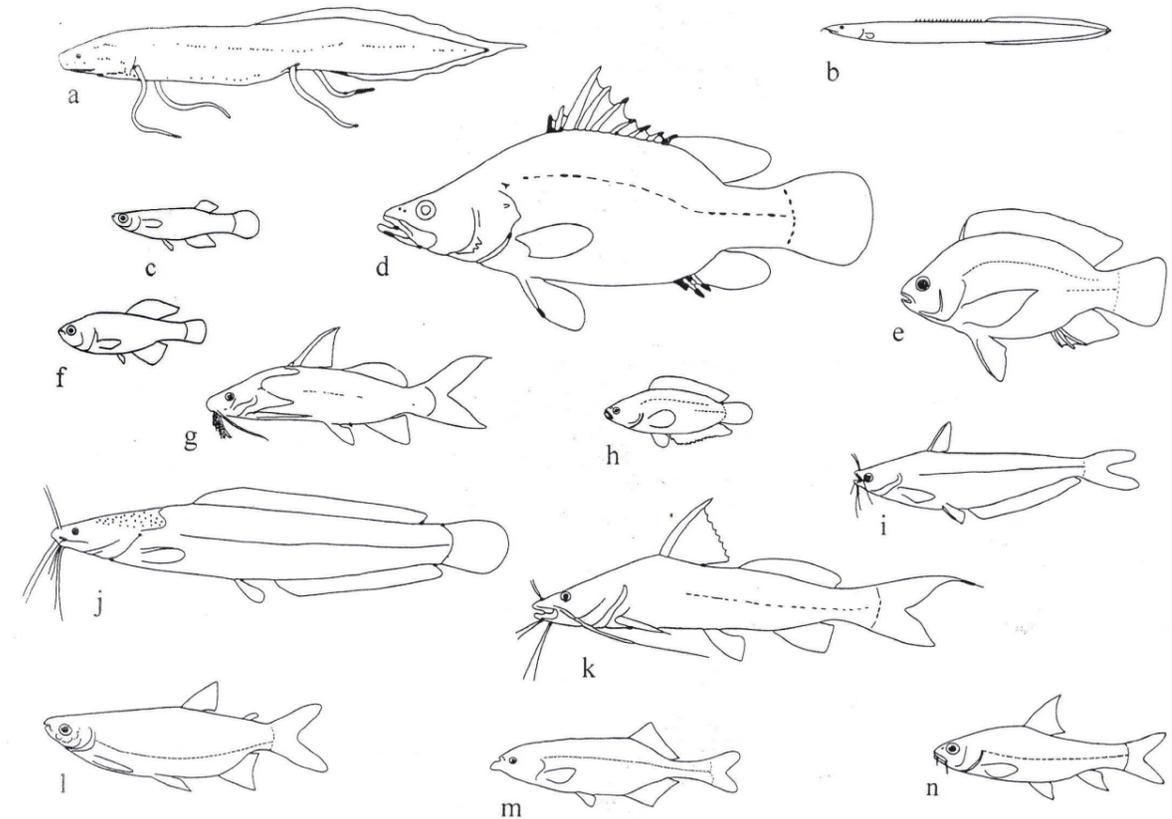
Fig. 1. Outline figures of representatives of the fish families in Lake Victoria. a, Protopteridae; b, Mastacembelidae; c, Poeciliidae; d, Latidae; e, Cichlidae; f, Nothobranchidae; g, Mochokidae; h, Anabantidae i, Schilbeidae; j, Clariidae; k, Bagridae; l, Alestidae; m, Mormyridae; n, Cyprinidae (after van Oijen 1995).

Figure 3. Haplochromine trophic groups from Lake Victoria: (**a**) species composition in all habitats. Note that the paedophages and the scale scraper are included in the piscivores and that rare trophic types, like the parasite feeders and a crab eater, are not included; (**b**) biomass composition in sub-littoral waters (6-20 m deep; from Witte *et al.* 2009a).

Fig. 2. Changes during the 1970s and 1980s in (**a**) total fish landings in the Tanzanian part of Lake Victoria and (**b**) demersal fish stocks in the Mwanza Gulf (Tanzania) calculated from bottom trawls catches. The decline of haplochromines in the bottom trawl catches in the Mwanza Gulf in the period 1973-1984 was mainly due to trawl fishery; the subsequent further decline was caused by the Nile perch upsurge. Note that bottom trawls did not catch the small pelagic *Rastrineobola argentea*. After 1985, Nile tilapia dominated the tilapiine catches (after Witte *et al.* 1999).

Several authors have raised doubts about the taxonomic status of Lake Victoria haplochromines (e.g. Sage & Selander 1975; Meyer 1987). However, ecological research corroborated in many cases the biological soundness of species distinction originally based on male colouration and small morphological differences; viz. no indications of gene flow could be found between presumed species that live in sympatry (Hoogerhoud *et al.* 1983; Goldschmidt & Witte 1990; Seehausen *et al.* 1998, 2008).

Molecular studies suggest that the 500+ haplochromine species of Lake Victoria evolved within the geologically short period of 100,000-400,000 years (Meyer *et al.* 1990; Nagl *et al.* 2000; Seehausen *et al.* 2003; Verheyen *et al.* 2003). However, paleolimnological data indicate that Lake Victoria was completely dry between 18,000 and 15,000 years ago (Johnson *et al.* 1996; Stager & Johnson 2008). The discrepancy between these data resulted in vigorous debates about the origin, age, and evolutionary history of the extraordinary speciose Lake Victoria haplochromines (e.g. Nagl *et al.* 2000; Seehausen *et al.* 2003; Verheyen *et al.* 2003; Fryer 2004; Seehausen 2006; Elmer *et al.* 2009). Nagl *et al.* (2000) suggested that the Lake Victoria haplochromines originated from trophic generalists, which lived in the East-African river systems and in which mutations for morphological adaptations were already present as polymorphisms. Data of Seehausen *et al.* (2003) indicated that the Lake Victoria –Edward flock is derived from the morphologically and ecologically diverse cichlid genus *Thoracochromis* from the Congo and Nile. Verheyen *et al.* (2003) explained the fast radiation of eco-morphological diversity in Lake Victoria haplochromines by their descent from the lacustrine, possibly already diversified, Lake Kivu ancestors, a view confirmed by Elmer *et al.* (2009). All these papers suggest that the Lake Victoria cichlid flock sensu stricto must be older than 15,000 years, and is not strictly monophyletic. Elmer *et al.* (2009) estimated that the most recent common ancestor of the cichlids of lakes Victoria, Albert, Edward, George, Kivu and Kyoga together (the Lake Victoria region 'super flock') existed about 4.5 million years ago. They also suggest that the Pleistocene desiccation 'bottlenecked but did not extirpate' the adaptive radiation of Lake Victoria haplochromines.

Rapid speciation has been suggested to be a typical feature of haplochromine cichlids (Seehausen 2006) and is thought to be mainly the result of sympatric

speciation through disruptive sexual selection for conspicuous coloration (Maan *et al.* 2004; Seehausen *et al.* 2008) and strong assortative mating (Seehausen & van Alphen 1998). Learning in the form of sexual imprinting seems to facilitate assortative mating and reproductive isolation among closely related cichlid species (Verzijden & ten Cate 2007).Water clarity appears to be important for this mode of speciation, and there is a significant correlation between the number of coexisting haplochromine species and transparency among different East African lakes and among localities within Lake Victoria (Seehausen *et al.* 1997a; Mrosso *et al.* 2004).

Apart from sympatric speciation through disruptive *sexual* selection, sympatric ecological speciation by disruptive *natural* selection for resources may have played a role. A potential example concerns the species pair *H. piceatus* Greenwood & Gee, 1969 and *H. coprologus* Niemantsverdriet & Witte, 2010. These species have a similar male colouration, but *H. coprologus*, which used to feed on detritus and phytoplankton, was more deep bodied and had a longer intestine than *H. piceatus* with a diet of zooplankton and insect larvae (De Zeeuw *et al.* 2010). Furthermore, they differed in depth distribution and spawning sites (Goldschmidt *et al.* 1990, 1993; De Zeeuw *et al.* 2010). Sympatric ecological speciation by disruptive natural selection for resources has also been suggested for the cichlid species flock in the Crater Lake Barombi Mbo in Cameroon (Schliewen *et al.* 1994) and for the Lake Tana barbs (Sibbing *et al.* 1998). Finally, allopatric speciation in satellite lakes, that later became connected again to the main lake, probably contributed to species diversity as well (Greenwood 1965, 1974; Kaufman *et al.* 1997). Seehausen (2000) stressed that 'the evolution of species diversity requires three processes: speciation, ecological radiation and anatomical diversification…'. The functional decoupling of the upper and lower pharyngeal jaws in cichlid fish may have contributed to the third process and may explain the high degree trophic radiation of the haplochromines (Galis & Drucker 1996). However, as Seehausen (2000) suggested, the high degree of phenotypic plasticity in cichlids (e.g. Witte *et al.* 1997), possibly also played a role.

Human induced changes
Fishery in Lake Victoria before the Nile perch boom
In a report on a lake-wide expedition in 1928, Graham (1929) provided an extensive description of the

fishery in Lake Victoria. Perhaps with the exception of scoop nets, netting material was not used in the traditional fishing techniques in Lake Victoria (Graham 1929). Flax gill nets from Europe had been introduced in 1905, but traps, baskets and moving papyrus fences (operated as a kind of seine) were still frequently used in 1928. Even in the 1970s and 1980s traps were still in use in some areas.

From the 1920s till the beginning of the 1950s, the most important food fish of the lake was the tilapiine cichlid *O. esculentus*, but other large fish species such as *O. variabilis*, the lungfish *P. aethiopicus* and the catfishes *C. gariepinus* and *B. docmak* were also fished (Graham 1929; Garrod 1960). In shallow water, women caught the small (< 10 cm total length, TL) cyprinid *R. argentea* by forming a circle, driving the fish to the centre and scooping them from the water with baskets (Graham 1929).

Apart from the widely appreciated *O. esculentus,* the preference for other fish species in Lake Victoria differed locally. For instance, because of its snake-like appearance, the lungfish was disliked by most Wasukuma people living on the south-eastern shores of the lake, but it was highly appreciated by the Wajuluo living around the Nyanza Gulf. The Wahaya and Baganda on the western and northern side of the lake considered *B. docmak* a delicacy. Haplochromine cichlids were popular as food fish among the Wakerewe at Ukerewe Island (Graham 1929; Witte *et al.* 1999).

Fishing down the food web
The introduction of modern fishing gear, like gill nets and beach seines, and the increased demands for fish because of the growing human population and the opening of new markets, due to new roads and railway connections, had a strong impact on the fish catches in the first half of the 20th century (e.g. Graham 1929; Beverton 1959; Fryer & Iles 1972; Balirwa *et al.* 2003; Balirwa 2007). Popular food fish such as *O. esculentus* and the cyprinid *Labeo victorianus* Boulenger, 1901, showed clear signs of over-fishing by the 1940s and 1950s respectively (Cadwalladr 1965; Fryer & Iles 1972; Fryer 1973). The introduction, after the Second World War, of the more catch efficient and long lasting nylon gill nets, and of outboard engines, further increased fishing pressure. The catch per night of native tilapiines in a 50 m-long 127 mm-mesh gill net, decreased from 50-100 fish in 1905 to < 0.5 fish in the same net in 1970 (Kudhongania & Cordone 1974). The minimum mesh size of

127 mm (5 inch) for gill nets was repealed in 1958, which resulted in a short revival and subsequent further dwindling of the catches. The changes in the Lake Victoria fish stocks between 1950 and 1980 conform in a general way to the fishing down model, viz. a dramatic decline in tilapiine catches, followed by a decline in large catfishes and lung fish and an increase in smaller taxa including haplochromine cichlids (Balirwa *et al.* 2003; Welcomme 2005).

Fishery for the small pelagic *R. argentea* using lamps to attract the fish developed in the 1960s and 1970s in Lake Victoria, and was derived from a similar fishery in Lake Tanganyika aiming at clupeids (Okedi 1981). Originally, fish were attracted by lamps attached to rafts that were hauled in slowly to the shore, where the fish were caught with small meshed beach seines. By the end of the 1980s, lift nets and encircling nets, which could be operated offshore, were used to catch the fish that had been attracted by the lamps (Ligtvoet *et al.* 1995).

A lake wide trawl survey in 1969 estimated the standing stock of haplochromine cichlids at 600,000 t (80 % of the demersal fish stock in the lake), and it was suggested that 200,000 t y[-1] could be harvested (Kudhongania & Cordone 1974). Ways were sought to exploit this major fish source. Bottom trawling for haplochromines as supply for a fishmeal factory in Mwanza started in the Tanzanian waters in 1976. This factory converted some 10-15 t of haplochromines per day into animal fodder, and signs of local over-fishing of haplochromines in the Mwanza area were reported within a few years (Fig. 2b; Witte & Goudswaard 1985).

Species introductions
To improve the dwindling catches, several fish species were introduced into Lake Victoria in the 1950s (Welcomme 1988). They comprised the Nile perch (*L. niloticus*), Nile tilapia (*O. niloticus*) and the tilapiines *O. leucostictus* (Trewavas, 1933), *Tilapia zillii* (Gervais, 1848) and *T. rendalli* Boulenger, 1896. In the 1980s Nile perch suddenly boomed in Lake Victoria and, concomitantly, the haplochromine cichlids in the sub-littoral and offshore areas vanished almost completely (Fig. 2; Barel *et al.* 1985, 1991; Ogutu-Ohwayo 1990a; Witte *et al.* 1992). These included areas where haplochromines had been fished and already declined, but also areas where there was no fishery on haplochromines. Other species, like the introduced Nile tilapia and especially the native *R. argentea* increased in biomass in the presence of the

Nile perch (Wanink 1999; Goudswaard *et al.* 2002b). The biomass of *R. argentea* increased approximately by a factor of four, but the increase in numbers was about double as high due to a decrease in size of this small cyprinid (Wanink 1999). This strong increase in catch may have been caused by competitive release with the former abundant (zooplanktivorous) haplochromines and a reduction in generation time (Wanink & Witte 2000a). Moreover, in contrast to haplochromines, *R. argentea* were mainly eaten by Nile perch in shallow water (< 12 m deep) but not in the deeper parts of the lake (Katunzi *et al.* 2006). A strong increase was also observed in the biomass of the shrimp *Caridina nilotica*, possibly due to a decreased predation pressure on juvenile shrimps by haplochromines (Goldschmidt *et al.* 1993; Goudswaard *et al.* 2006; Budeba & Cowx 2007b).

It took more than 25 years since the first release of Nile perch in Lake Victoria before a dramatic upsurge in the abundance and catch landings of Nile perch was observed. This may have been driven, at least in part, by high survival of very young Nile perch and the food abundance for these fishes. Goudswaard *et al.* (2008), suggested that the abundant haplochromines fed upon eggs and larvae of Nile perch, whenever available. Moreover, the haplochromines were probably competing with juvenile Nile perch for zooplankton and insect larvae. In contrast, a recent study found that the timing and speed of the Nile perch upsurge was not controlled by external triggers and simply grew exponentially (Downing 2012). Nile perch first became noticeably successful in the heavily exploited Nyanza Gulf, Kenya, in 1980. By the early 1970s, over-exploitation of haplochromines was already evident in this area (Marten 1979), which may have facilitated increased survival of juvenile Nile perch. During the subsequent expansion from the Nyanza Gulf towards other areas of the lake, the adult and sub-adult Nile perch fed heavily upon haplochromine cichlids (Hughes 1986; Ogutu-Ohwayo 1990a, b; Mkumbo & Ligtvoet 1992) and reduced their numbers to extremely low levels. This process, in some areas like the Mwanza Gulf accompanied by overfishing of haplochromines, likely enhanced survival of eggs and larvae of Nile perch. After the decline of the haplochromines and the upsurge of the shrimps, juvenile shrimps became an important food item for small (< 10 cm TL) Nile perch (Katunzi *et al.* 2006; Goudswaard *et al.* 2006). Thus, adult Nile perch may have facilitated the survival of their offspring by

eradicating haplochromines that were potential predators and competitors of juvenile Nile perch, but see Downing (2012). However, in some areas of the lake this seems to have been done by heavy fishing on the haplochromines (Goudswaard *et al.* 2008).

Thirty years after its introduction, Nile tilapia had become the most common tilapiine species in Lake Victoria. It replaced the overfished native tilapiines almost completely before the Nile perch came to dominate the ecosystem (Ogutu-Ohwayo 1990a; Goudswaard *et al.* 2002b). The main cause of the final disappearance of the native tilapiine species is presumed to be the competitive dominance of Nile tilapia (Lowe-McConnell 2000, Goudswaard *et al.* 2002b).

In 1989, the South American water hyacinth, *Eichhornia crassipes* (Martias) Solms, 1883 appeared in Lake Victoria. This new intruder quickly established itself (Njuguna 1991). For almost a decade extensive mats of this weed covered large areas along the lake's shores, depriving waters of light and oxygen. To eradicate the weed, locally mechanical removal was applied. Furthermore, South American weevils (*Neochetina eichhorniae* Warner, 1970 and *N. bruchi* Hustache, 1926), were introduced for biological control of the water hyacinth. In 1998 the water hyacinth strongly declined again. However, according to some authors this decline was not only due to the weevils, but also to El Niño events during 1997/1998 that resulted in extensive clouds, which reduced the light conditions and consequently plant growth (Williams *et al.* 2005, 2007). Moreover, shore bound mats were dislodged by raising water levels and driven to open water, where waves helped to destroy them. In the Mwanza Gulf densities of water hyacinth have fluctuated during the past decade, but they have not returned to the peak levels observed in the 1990s (MAKM, JHW and FW pers. obs.).

Environmental degradation and climate change
In the course of the 1980s, frequent blooms of cyanobacteria also became a common feature. They were the result of eutrophication due to the increased human population density, deforestation, and agriculture (Hecky 1993; Mugidde 1993; Scheren *et al.* 2000; Verschuren *et al.* 2002). Losses of phytoplankton through grazing by fish were less than 5% of daily gross and less than 15% of daily net phytoplankton production. As a consequence it is unlikely that the phytoplankton blooms in the second half of the 1980s were due to a top-down effect caused by the strong decline in phyto-

plankton grazing by fish (Witte *et al.* 2012). Eutrophication and algal blooms caused decreases in water transparency (Mugidde 1993, Seehausen *et al.* 1997a; Witte *et al.* 2005) and in dissolved oxygen levels (Ochumba & Kibaara 1989; Kaufman 1992; Hecky *et al.* 1994; Wanink *et al.* 2001). Sudden upwelling of hypoxic water caused mass fish kills (Ochumba & Kibaara 1989; Ochumba 1990; Kaufman 1992; Kudhongania & Chitamwebwa 1995; Wanink *et al.* 2001; Goudswaard *et al.* 2011). The wetland zone that regulates material transport to the lake has also been under intense pressure from human activities (Balirwa 1995; Kairu 2001). Clearing of papyrus (*Cyperus papyrus* Linnaeus 1753) fringes along the lake shore and conversion of wetlands into agriculture land may have contributed to the decline of lungfish by destroying their breeding habitat (Goudswaard *et al.* 2002a). It has been suggested that water hyacinth mats, which are common since the 1990s, provided a suitable habitat for lungfish and that it played a role in their resurgence in the second half of the 1990s (Bugenyi & Van der Knaap 1997).

Climate change may also have been one of the stressors that affected Lake Victoria (Hecky *et al.* 2010). In the 1990s, the lake was warmer than in the 1960s with a shallower, more stable and more persistent thermocline, which contributed to the deoxygenation of deep water (Hecky 1993; Hecky *et al.* 1994, 2010). Low wind stress that was measured from the mid 1970s to the mid 1990s in Lake Victoria could also have contributed to the longer and more stable anoxic layers (Kolding *et al.* 2008).

LAKE VICTORIA AFTER THE 1980s

Decline of fish diversity
The boom of the introduced Nile perch in the 1980s as well as fishery and habitat deterioration had a strong impact on the haplochromine cichlids and many other fish species (Ogutu-Ohwayo 1990a; Witte *et al.* 1992; Goudswaard & Witte 1997; Goudswaard *et al.* 2002a, b, 2008). It was estimated that some 200 of the endemic haplochromine species may have gone extinct (Witte *et al.* 1992). The highly structured rocky shores and papyrus fringes, where Nile perch densities are low, were less affected by Nile perch than the sub-littoral and offshore waters (Witte *et al.* 1992, 2007a; Seehausen 1996). However, the decrease in water transparency due to eutrophication may have caused hybridization among several haplochromine

species, including those living along rocky shores (Seehausen *et al.* 1997a, 2008; Seehausen 2006). Lake Victoria haplochromines are rather tolerant of low oxygen concentrations (Verheyen *et al.* 1986; Chapman *et al.* 1995; Rutjes *et al.* 2007), therefore the impact of the increased hypoxic conditions due to eutrophication (Hecky *et al.* 1994) may have been less severe than suggested (Witte *et al.* 2005).

Some satellite lakes of lakes Victoria and Kyoga were not invaded by Nile perch or affected by eutrophication. Apart from endemic haplochromine species, these satellite lakes contain some species that are the same as, or similar to, those that vanished from the main lakes; thus providing important refugia for some species and trophic groups (Kaufman & Ochumba 1993; Mwanja *et al.* 2001; Aloo 2003; Mbabazi *et al.* 2004).

Nile perch predation, competition with introduced species, habitat deterioration and fishing pressure also contributed to declines in other native species including catfishes [*B. docmak*, *Xenoclarias eupogon* (Norman, 1928), *Synodontis victoriae* Boulenger, 1906], the lungfish *Protopterus aethiopicus*, the mormyrid *Mormyrus kannume* Forsskål, 1775, the cyprinid *Barbus altianalis radcliffi* Boulenger, 1903 and the tilapiines *O. esculentus* and *O. variabilis* (Table 2; Goudswaard 1988; Ogutu-Ohwayo 1990a; Goudswaard & Witte 1997; Goudswaard *et al.* 2002a, b). However, the impacts of the above described human induced threats were not the same for all fish species. In several cases a threat to one species did have a positive effect on another species; e.g. the decline of haplochromines by Nile perch predation had a positive effect on the population of *R. argentea* (Table 2).

Resurgence of some haplochromine species
In the course of the 1990s, after a decline of Nile perch in Lake Victoria due to intensive fishing, a slow resurgence of some haplochromine species was observed in the sublittoral waters (Witte *et al.* 2000, 2007a, b; Balirwa *et al.* 2003; Getabu *et al.* 2003). Similar observations were made in Lake Nabugabo, a shallow satellite lake of Lake Victoria (Ogutu-Ohwayo 1993; Chapman *et al.* 2003).

The resurgence in Lake Victoria, mainly concerned zooplanktivorous and detritivorous haplochromines, but of each group only about 30% of the species recovered, and initially the ratio in biomass of detritivores and zooplanktivores was reversed (Witte *et al.* 2007a, b). Before the 1980s detritivores made up about 50% of the haplochromine biomass in the sublittoral waters

Table 2. Human induced changes and their impacts on various fish stocks (neg = negative; pos = positive).

Change	impact	on:
Increased fishery	neg	Most fish species (esp. native tilapiines + large cyprinids) and finally on Nile perch
Increased Nile perch	neg	Most fish species (esp. haplochromines), but not on *R. argentea* and Nile tilapia
Increased Nile tilapia	neg	Native tilapiines
Habitat deterioration	neg	Lungfish + *C. gariepinus*?
Increased eutrophication	neg	Especially haplochromines (hybridization)
Increased water hyacinth	pos	Lungfish and *C. gariepinus* and possibly some other fish species that could cope with low oxygen levels and limited light conditions
Decreased haplochromines	pos	Juvenile Nile perch, shrimps and *R. argentea*

Table 3. Preliminary data on ecological and morphological changes in resurging detritivorous (Detr), zooplanktivorous (Zoo) and oral shelling molluscivorous (Or sh) haplochromine species. Numbers represent the number of species in which the changes were observed. Note that absence of changes may imply that no changes were observed or that the trait has not yet been studied.

Trophic group (number of species)	Detr (2)	Zoo (3)	Or sh (1)	Sources
Trait				
Habitat change	2	3	1	1, 2, 3
Increased fecundity	-	3	-	4, 5
Diet	2	3	1	1, 6, 7, 8, 9
Intestine length	2	-	-	8
Head volume	-	3	-	10, 11
Body shape	1	3	1	12
Eye size	-	3	1	10, 12, 13
Retina	-	2	-	13, 14
Muscles feeding app	-	1	-	10
Dentition premaxilla	-	2	1	9
Gill raker number	-	1	-	11
Gill surface area	-	2	1	10, 11

Sources = [1]van Oijen & Witte 1996; [2]Seehausen et al. 1997b; [3]Kishe-Machumu 2012; [4]Wanink 1991; [5]JHW unpublished; [6]Wanink 1998; [7]Katunzi et al. 2003; [8]Kishe-Machumu et al. 2008; [9]Van Rijssel et al. submitted; [10]Witte et al. 2008; [11] JCVR unpublished; [12]Van Rijssel & Witte 2013; [13]Van der Meer et al. 2012; [14]Witte et al. 2005.

of the Mwanza Gulf and zooplanktivores about 25% (Fig. 3b; Goldschmidt et al. 1993), whereas by 2005 detritivores constituted only 26% and zooplanktivores more than 70% (Witte et al. 2007a). In 2008 and in February - April 2011, detritivores were the dominant group again (Kishe-Machumu 2012; MAKM, JCVR and FW pers. obs.). However, the majority of the species did not recover (Witte et al. 2007a). In spite of frequent sampling in the Mwanza Gulf in the period between 1987 and 2011, many of the highly specialized trophic types like scale eaters, parasite eaters and prawn eaters have not been caught, whereas piscivores and paedophages are extremely rare now, both with respect to numbers of individuals and species. Similar results were found by Mizoiri et al. (2008) who sampled the Mwanza Gulf and the Speke Gulf at many localities in 2004, 2005 and 2006.

Nile perch longer than 20 cm total length, which since the disappearance of the haplochromine cichlids mainly fed on shrimps, its own juveniles and *R. argentea* (Hughes 1986; Ogutu-Ohwayo 1990b; Mkumbo & Ligtvoet 1992; Katunzi et al. 2006), switched again to haplochromines after their re-emergence (Budeba & Cowx 2007a; Kishe-Machumu et al. 2011).

Responses to environmental changes

Apparent responses to the environmental changes were observed in several fish species in the Mwanza Gulf. Some haplochromine species extended their use of habitat (Table 3). Most striking were the zooplanktivorous *Haplochromis (?) tanaos* van Oijen & Witte, 1996 and the snail shelling *Haplochromis (Paralabidochromis) plagiodon* Regan & Trewavas, 1928, which formerly were restricted to the shallow (< 6 m) sand stations in Butimba Bay. Since the resurgence of the species in the 1990s, both occur predominantly over mud bottoms up to 11 m depth (Seehausen et al. 1997b; Kishe-Machumu 2012; MAKM, JHW, JCVR and FW unpublished data). In contrast the zooplanktivore *Haplochromis (Yssichromis) pyrrhocephalus* Witte & Witte-Maas, 1987 now also occurs in shallower areas than in the past. Reproductive strategies changed in the Nile tilapia (Ojuok et al. 2007) and the cyprinid *R. argentea* (Wanink & Witte 2000a; Manyala & Ojuok 2007); both have shown a decrease in their size at maturity. In the zooplanktivorous haplochromines, *Haplochromis (Yssichromis) laparogramma* Greenwood & Gee, 1969, *H. pyrrhocephalus* and *H. tanaos*, an increase of both absolute and relative fecundity have been observed (Wanink 1991; Wanink & Witte 2000a; JHW unpublished data).

Dietary shifts were observed in zooplanktivorous and detritivorous/phytoplanktivorous haplochromines (van Oijen & Witte 1996; Katunzi et al. 2003; Kishe-Machumu et al. 2008; van Rijssel et al. submitted) as well as in the oral shelling haplochromine *Platytaeniodus degeni* Boulenger, 1906 (van Rijssel et al. submitted). In all these cases the amount of macroinvertebrates in the diets increased strongly. Similar changes in diet were found in other fish taxa (Table 4). These changes were also reflected in comparisons of stable isotopes of detritivorous and zooplanktivorous haplochromines between the pre- and post-Nile perch

Table 4. Dominant food items in diets of different fish taxa from Lake Victoria before and after the ecological changes in the 1980s.

Taxon	before 1980s	1990s -2006
Zooplanktivorous hapl. (3 sp.)[1,2,3]	zooplankton	Macroinvertebrates (+zoopl)
Detritivorous hapl. (> 3 sp.)[4]	detritus/phytoplankton	macroinvertebrates
Platytaeniodus degeni[3]	detritus (+ molluscs)	macroinvertebr (+ molluscs)
Bagrus docmak[5]	haplochromines	insects, *R. argentea*
Schilbe intermedius (Linnaeus, 1758)[5]	haplochromines	insects
Rastrineobola argentea[6,7]	zooplankton	macroinvertebr, fish
Brycinus sadleri (Boulenger, 1906)[8]	plants, insects	macroinvertebrates
Nile tilapia[7,9,10,11]	detritus/phytoplankton	macroinvertebrates

[1] van Oijen & Witte 1996; [2]Katunzi et al. 2003; [3]Van Rijssel et al. submitted; [4]Kishe-Machumu et al. 2008; [5]Olowo & Chapman 1999; [6]Wanink 1998, [7]Budeba & Cowx 2007a; [8]Wanink & Joordens 2007; [9]Gophen et al. 1993; [10]Bwanika et al. 2006; [11]Njiru et al. 2007.

era (Kishe-Machumu 2012). In the detritivorous/phytoplanktivorous haplochromines the shift in diet was accompanied by a decrease of 30% in relative intestine length (Kishe-Machumu *et al*. 2008). As discussed by Kishe-Machumu *et al*. (2008) potential factors for these diet shifts could be: (a) the increased availability of profitable food items; (b) the loss of competitors, and (c) the increased water turbidity after the environmental changes. In the last case, it is supposed that the fish that grew up under low light conditions changed their retina in such a way that they increased their light sensitivity at the cost of their resolution (e.g. Van der Meer 1993; Van der Meer *et al*. 2012).

Some resurgent zooplanktivorous species showed body shape changes as a response to the environmental changes while other zooplanktivores, which are thought to be extinct or poorly recovered, showed changes in the opposite direction (Van Rijssel & Witte 2013). One of the resurgent species is the zooplanktivorous *H. pyrrhocephalus* which is currently the most common haplochromine cichlid in the Mwanza Gulf, and its morphology has been studied extensively. A comparison of specimens collected in the 1970s (pre-Nile perch population) and those collected in the 1990s (modern population) revealed that head length and head volume (for *H. pyrrhocephalus*) decreased in three different haplochromines (Witte *et al*. 2008; Van Rijssel & Witte 2013). These size decreases match biomechanical predictions for increased swimming speed in presence of predators (Langerhans *et al*. 2004, Chapman *et al*. 2008). The gill surface area in resurgent *H. pyrrhocephalus* increased by 64%, which is an apparent adaptation to the increased hypoxic conditions. The gill rakers decreased in length and the cheek depth and the *musculus levator* posterior, responsible for biting force of the pharyngeal jaws, increased in size (Witte *et al*. 2008). These changes may reflect adaptive responses to the larger and tougher prey types in the diet of modern *H. pyrrhocephalus* (Katunzi *et al*. 2003). Reductions in eye size and in the size of the *musculus sternohyoideus*, and reallocation of space among compartments of the head seem to have permitted accommodation of larger gills in a relatively smaller head (Witte *et al*. 2008).

A reduction in eye size was also observed in *H. tanaos*. However, it was also observed that while the density of the blue sensitive single cones were reduced, the size of the red and green cones in the retina had increased (Witte *et al*. 2005; Van der Meer *et al*. 2012). In eutrophied water with high algae concentrations,

blue light is filtered out faster than red and green light. So, blue sensitive cones may be of reduced relevance in the current visual habitat of *H. tanaos*. In spite of its reduced eye size, light sensitivity was probably improved by the increased size of the double cones, but at the cost of the resolving power. However, as it currently feeds on larger prey, the loss of resolution may not have much impact on feeding performance of *H. tanaos*. Finally, preliminary studies suggest changes in oral dentition in several of the recovering species, which also may be related to the change in diet (Van Rijssel *et al*. submitted)

Though less striking than in the haplochromine cichlids, morphological changes were also observed in the cyprinid *R. argentea*; the number of gill filaments increased, whereas the number of gill rakers decreased, possibly in response to the lower oxygen concentrations and larger prey, respectively (Wanink & Witte 2000b).

The rapid morphological changes described above may reflect environmentally induced plasticity, heritable response to natural selection, genetic introgression through hybridisation or, most likely, a combination of several of these factors. Recent studies of contemporary evolution in natural populations, especially in response to environmental changes caused by human activity, yielded estimates of potential rates of evolution many orders of magnitude greater than rates inferred from the fossil record (e.g. Carrol *et al*. 2007).

Fishery in Lake Victoria after the Nile perch boom

By the end of the 1980s only three fish species were common in sub-littoral and offshore waters of Lake Victoria. These were the small indigenous cyprinid *R. argentea* and the introduced Nile perch and Nile tilapia (Fig. 2a; Ogutu-Ohwayo 1990a; Wanink 1999; Goudswaard *et al*. 2002b). Together, they dominated the fish landings by more than 80% (Fig. 2a; Reynolds *et al*. 1995).

Although biodiversity decreased strongly and water quality deteriorated, fish production in Lake Victoria flourished after the Nile perch boom. In the 1960s, the total landings for the lake were approximately 100,000 t y⁻¹. In the late 1980s and early 1990s, just after the Nile perch boom, the fisheries produced over 500,000 t of fish annually (Balirwa 2007). Concomitantly, bottom trawl catches revealed that the standing stock of demersal fish had decreased about five times (Fig.2 b; Okaronon 1994; Witte *et al*. 1999; Balirwa 2007). This indicates that the dramatic increase of the

total fish landings reflected an increase in fishing effort, which was indeed observed during the past decades (Ogutu-Ohwayo 2004; Matsuishi *et al*. 2006; Balirwa 2007). The number of fishers and fishing boats tripled between 1990 and 2007 (Fig. 4; Ogutu-Ohwayo 2004; Matsuishi *et al*. 2006; Mkumbo *et al*. 2007). Since the1980s, the total annual landings in the lake increased, but by the mid 1990s the contribution of Nile perch showed some decline, whereas landings of *R. argentea* and Nile tilapia increased (Fig. 4; Matsuishi *et al*. 2006). Just after the boom, Nile perch contributed more than 70% to the fish landings (Figs 2, 4; Van der Knaap *et al*. 2002), but between 1990 and 2000 the catch per unit effort of Nile perch dropped from about 80 to 45 kg per boat per day in the Kenyan waters, where adequate data had been collected (Matsuishi *et al*. 2006). By 2000 the total annual landings amounted to 657,000 t, 40% of which was made up by Nile perch, 41% by *R. argentea* and 8% by Nile tilapia (calculated from Table 1 in Matsuishi *et al*. 2006). The landings of haplochromine cichlids had increased from virtually zero at the end of the 1980s to 17,000 t y⁻¹ in the Tanzanian waters and to 4,000 t y⁻¹ in the Ugandan waters, whereas in Kenyan waters the catches were only 300 t y⁻¹ (Matsuishi *et al*. 2006).

In the period 2005-2007, the annual landings were even estimated at 1 million t and the contribution of Nile perch was about 26%, while that of *R. argentea* had increased to about 53% (Fig. 4, LVFO, CAS Report 2006). Apparently, the species composition in the fish landings has changed toward lower trophic level species (viz. *R. argentea* and Nile tilapia, Matsuishi *et al*. 2006). Hydroacoustic surveys between 1999 and 2008 suggested that over the studied period the overall fish biomass in Lake Victoria remained more or less constant, but the biomass of Nile perch decreased, whereas that of *R. argentea* increased (Fig. 5; Getabu *et al*. 2003; Mkumbo *et.al* 2005; LVFO Hydroacoustic Survey Report 2007; LVFO, IFMP 2, 2008; Kayanda *et al*. 2011). The foregoing seems to represent a second fishing down episode in Lake Victoria (Balirwa *et al*. 2003).

Originally, the fishermen did not like Nile perch because they had problems with handling, processing and marketing the fish; the larger and relatively fat perch could not easily be dried or transported. However, in the years after the upsurge, people rapidly adjusted the processing and transport techniques. The larger fishes were chopped into pieces and subsequently fried in the fat removed from the intestines
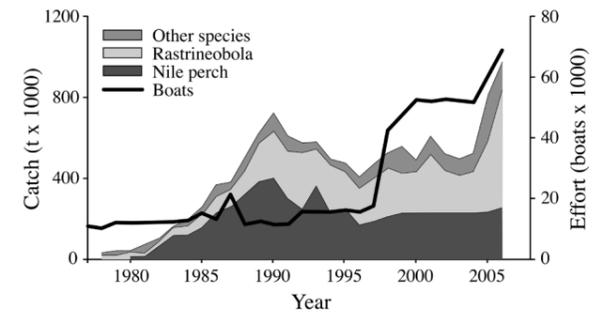
Fig. 4. Trends in total annual fish landings and total fishing effort in Lake Victoria during the period 1975 – 2005. Nile tilapia is included in 'other species'. Note that the increase in effort was mainly directed at Nile perch (effort data from LVFO Frame Survey Report, 2006; Catch data from LVFO IFMP 2, 2008; Figure from Witte *et al*. 2009b).

(Ligtvoet 1989; Ligtvoet *et al*. 1995). The smaller ones were dried in the sun or smoked. For frying and smoking firewood was needed, thus the Nile perch boom strongly exacerbated the ongoing deforestation along the lake shore. In the 1990s filleting factories arose for export of Nile perch fillets to Europe and Asia (Ntiba *et al*. 2001). The total capacity of these factories is several hundred tons per day, and they became the main buyers of Nile perch. Many of these fish processing plants now operate below their installed capacity. Balirwa (2003) reports that in Uganda, 15 factories with a total installed capacity of 420 t per day, are actually processing 185 t per day. Currently, about 1.2 million people are directly or indirectly dependent for their livelihood on the fishery in Lake Victoria (Matsuishi *et al*. 2006). In 2003 the estimated annual catch was worth at least US$ 540 million at the fish landings, whereas a further US$ 240 million was
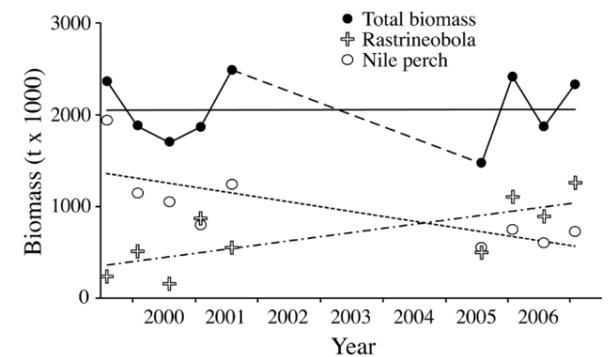
Fig. 5. Estimated fish biomass in Lake Victoria based on acoustic surveys in the periods 1999-2001 and 2005-2007. Note that the equipment and analytical protocols differed between the periods1999–2001 and the period 2005-2007 (after LVFO, Hydroacoustic survey Reports 2006 & 2007; Figure from Witte *et al*. 2009b).

earned in fish exports (Balirwa 2007).

Several observations, e.g. the decline in annual landings and the decline in size at first maturity, suggest that Nile perch is intensively fished, which may result in overexploitation. Consequently, it has been suggested that, under the scenario of increased fishing effort, the Nile perch fishery is unsustainable (Pitcher & Bundy 1995; Mkumbo 2002; Matsuishi *et al.* 2006; Mkumbo *et al.* 2007; Kayanda *et al.* 2011). However, according to Kolding *et al.* (2008) not over-fishing, but the ongoing eutrophication is the main threat to the Nile perch fishery. Based on Chl α measurements by Silsbe *et al.* (2006) and annual Nile perch catches, Kolding et al. (2008) suggest that the top of the productivity curve for Nile perch as a function for eutrophication has been reached.

In the past, the management measures governing Lake Victoria resources were different in each country (Ntiba *et al.* 2001). Through the Lake Victoria Fisheries Organization (LVFO) that was formed in 1994 and support from the EU to implement a Management Plan, attempts to harmonize policies and regulations and also to develop standard operational procedures are continuing. Lake-wide management regulations are established, and a co-management approach has been adopted. About 1060 Beach Management Units (BMUs) have been established around Lake Victoria to take an active role in management of the resources at beach level (LVFO Website www.lvfo.org). The harmonized rules include: banning of beach seines, bottom trawls and cast nets, and of gill nets below 13 cm (5 inches) mesh size; as well as implementation of a slot size of 50 to 85 cm total length for Nile perch (Kizza *et. al.* 2005).

CONCLUSION

Dramatic changes occurred in the ecosystem and fish fauna of Lake Victoria during the past century as a result of human activities in and around the lake. The Nile perch boom altered the biomass distribution over trophic levels from a pyramid shape at the end of the 1970s to a top-heavy shape at the end of the 1980s, while by 2005, the pyramid shape was regained again (Downing *et al.* 2012). Nevertheless, many species, especially among the haplochromine cichlids, declined or even disappeared. Still there is hope for the future as a resurgence of some haplochromine species has been observed. Balirwa *et al.* (2003) suggested that conservation of biodiversity and fishery sustainability may not be in conflict in the management of Lake Victoria. A modelling study suggested that Nile perch prefer and grow fastest on a haplochromine prey base (Kaufman & Schwarz 2002). If the model is realistic, it would suggest that it is worth thinking of management strategies that allow sufficient fishing on Nile perch to ensure an abundance of their haplochromine prey, but not so much pressure as to threaten the Nile perch stock itself (Balirwa *et al.* 2003). However, to allow maintenance and restoration of haplochromine diversity and of other fish species, the urgent measures must include serious attempts to reverse the eutrophication of Lake Victoria (Seehausen *et al.* 1997a; Balirwa *et al.* 2003; Witte *et al.* 2005; Kolding *et al.* 2008).

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African Fresh and Brackish Water Fish Biodiversity and their Distribution: more unknowns than knowns

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ABSTRACT

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A short overview of the major ichthyogeographic provinces of Africa and Madagascar is given, highlighting some characteristics of the fish fauna of the region and the challenges ahead. Then a selection of current and future challenges in studies on the African fresh and brackish water fish diversity is discussed, showing that although more collections become available and methods more powerful, the unknowns still largely outweigh the knowns for our knowledge on one of Africa's most valuable natural resources, its unique fish diversity.

Keywords: ichthyology, taxonomy, biogeography, Afrotropical region

INTRODUCTION

Not unexpectedly, the first major ichthyogeographic reflections on the African freshwater fishes were made as soon as enough knowledge had accumulated to allow for comparisons between regions. While some notes and considerations had been published before, it was Boulenger (1905) who launched the first proper analysis. Boulenger, who was a Belgian ichthyologist employed at the then British Museum (Natural History) in London, pioneered the study of African fishes that became available to him at the time of the large European explorations in Africa and through colonial networks. This perhaps made Boulenger the last ichthyologist to have been able to have a thorough first-hand knowledge of (nearly) all African freshwater fishes known at a certain era. Boulenger (1905) briefly discussed the various families, their origin, affinities and distribution, and then discussed the five sub-regions he discerned, including a northern Palaeartic region, a southern region south of the Zambezi, and Madagascar. The remaining and major part of Africa was then split into a western-central sub-region and an eastern sub-region.

Further ichthyogeographic accounts were compiled (e.g. Pellegrin 1912; Poll 1973), while several regions were analysed from an ichthyogeographical point of view by various other authors (e.g. Thys van den Audenaerde 1963).

Roberts (1975) compiled all available information and provided a first major modern synthesis of the ichthyogeography of African fish fauna. His division and methodology was discussed and refined by Greenwood (1983). These contributions still form the basis for the current ichthyogeographic subdivision of the continent (see below), though various accounts have been published since then, too many to be cited in this introduction, dealing with the distribution of African freshwater fishes in general, the fishes of individual regions, the redefinition of a region, or a revision of fish groups. For an historical account of African freshwater ichthyology, we refer to Thys van den Audenaerde (2007), Paugy (2010) and Skelton & Swarts (2011).

A special effort to subdivide the major regions into smaller units was published by Thieme *et al.* (2005). The proposed regions resulted from a consensus opinion of experts on various major freshwater groups, including fishes. These regions are now regularly being discussed and a great deal of their current

use lies in the fact that the delineations of the regions proposed can be considered as testable hypotheses in review studies. As such, the book contains useful information to refine the existing borders of the various traditional ichthyogeographic provinces.

Before we move into the discussion of these provinces, it should be stressed that even the number of species currently considered valid from the African freshwaters is not known. Part of the problem is of course that the division between fresh, brackish and marine waters is not sharp, and neither is the boundary between their fish communities.

The Check-List of Freshwater Fishes of Africa (CLOFFA; Daget *et al.* 1984, 1986a&b, 1991) included 2,908 species from the African continent, Madagascar and its neighbouring islands. Boden *et al.* (2004) reported about 3,100 species from the Ethiopian realm (= Sub-Saharan Africa and Madagascar and the South Arabian Peninsula). In the recent IUCN red list assessment of African freshwater fish species (excluding Madagascar) 2,836 species were assessed (Snoeks *et al.* 2011). Early 2013, the FishBase team of the RMCA recorded 3,467 species that were reported from freshwaters in Africa and Madagascar in FishBase (Froese & Pauly 2013). What is certain is that the inventory is unquestionably far from complete, with many hundreds of species, maybe even over 1,000, still needing to be discovered and described.

In the following paragraphs, the major ichthyogeographic provinces and some of their characteristic features are discussed (Fig. 1). We will briefly touch upon some of the knowns and unknowns of each of these regions and their fish diversity. This review should not be regarded as a comprehensive state of affairs, as this is simply not possible within the current appraisal. It rather mentions and illustrates a number of issues discussed and concerns raised during the plenary lecture at the PAFFA meeting in Addis Ababa and these are limited to taxonomic and biogeographic topics.

THE MAGHREB

The Maghreb province, from various biogeographical points of view, does not have much in common with the other regions of the African continent. As such, and certainly from an ichthyogeographical point of view, it is not part of the Afrotropical region. Its fish fauna, dominated by cyprinids (Doadrio 1994), is rather Mediterranean and already Boulenger (1905) stated that it belongs to the Palearctic Realm.

THE NILO-SUDAN AND THE UPPER GUINEA

These two ichthyogeographic provinces are grouped together here for pragmatic reasons and jointly constitute the largest region, encompassing a few coastal rivers flowing into the West Indian ocean in Somalia, the major part of the Nile system in the north-east, the endorheic Lake Chad system, and the coastal rivers from Senegal on the border with Mauritania and Senegal eastwards to beyond the Niger delta. The Cross is regarded as the river bordering the Nilo-Sudan and the Lower Guinean ichthyogeographic provinces. To the north, this region is bordered by a zone that is not attributed to any province and which includes the Sahara desert. Probably it should be envisaged that the border of the Nilo-Sudan province in its western part at least should be shifted to the north to accommodate the typical Nilo-Sudanian species living in the small water bodies in the Sahara (cf. also Lévêque 1990).

The part taken up by the Upper Guinean Province in this large region is relatively small, but its delineation is not yet resolved (Fig. 1). We have adopted the borders as outlined by Lévêque (1997). We noticed a consensus in the literature to include at least the coastal areas from south of the Kogon river in Guinea eastwards to Liberia (Lévêque 1997). However, the extent of the area to the east and its presence or not within the Upper Guinean Province is a matter of debate, as is the influence of the so-called Baoulé V and the Dahomey gaps that in the past may or may not have formed barriers to fish distribution (see e.g. Howes & Teugels 1989; Hugueny & Lévêque 1994; Reid 1996). Currently the so-called Eburneo-Ghanaian region (Fig. 1, dotted area a) is considered to be part of the Nilo-Sudan Province.

Information on most of the fishes living in the area can be found in the comprehensive reviews on the fish fauna of West Africa (Paugy *et al.* 2003). These two volumes contain keys, descriptions and distribution maps of 584 species, as a result of a major collaborative effort between experts from various institutes. West Africa is therefore one of the best-known regions in terms of its fish diversity. However, the presence of these faunal works can give the false impression that everything is well known. Indeed, recent studies have demonstrated that a lot of work still remains to be done. Taxonomic problems have been reported for the small '*Barbus*' from West Africa (Bamba *et al.* 2011), the *Synodontis schall* complex (Musschoot & Laléyé 2008) and

Fig. 1. Map of Africa with ichthyogeographic regions (constructed using the Hydro1K elevation model shape files from the United States Geological Survey); based largely on Lévêque (1997) with modifications for lakes Rukwa, Kivu and Edward as in Snoeks *et al.* (2011). 1. Maghreb, 2. Nilo-Sudan, 3. Upper Guinea, 4. Lower Guinea, 5. Congo, 6. Quanza, 7. Zambezi, 8. Southern Province, 9. East Coast, 10. Madagascar. The Eburneo-Ghanaian (a) and the Abyssinian Highlands (b) are included in the Nilo-Sudan.

the African pike, *Hepsetus odoe* (Decru *et al.* 2012). One needs to take into account that these West African guides do not cover the whole area of the two provinces discussed above, as they did not include the Nilotic fauna. Lévêque & Paugy (1999) listed 127 from the Nile system excluding the area of the great lakes. This figure corresponds well to the 128 species mentioned by Witte *et al.* (2009) from the Nile River. Two more comments have to be made concerning the Nilotic system. First, Lake Albert is also considered to be part of the Nilo-Sudan region. It harbours some 48 species (Snoeks 2000), including some endemic

cichlids, while most non-cichlids are in common with the Nile. In addition, one special region of the Nile fauna should be highlighted here, the Abyssinian or Ethiopian Highlands. This region used to be regarded as a separate province but is now part of the Nilo-Sudan Province (Lévêque 1997; Lévêque & Paugy 1999). This region includes a unique species flock of large cyprinids in the Lake Tana system (Nagelkerke *et al.* 1994), the poorly known endemic *Afronemacheilus abyssinicus*, and represents a biodiversity hot spot for the cyprinid genus *Garra* (Stiassny & Getahun 2007).

THE LOWER GUINEA

This region extends from the Cross, a river shared with the Nilo-Sudan region (but see Hugueny & Lévêque 1994, who regard the Cross as Nilo-Sudanic), southwards to the mouth of the Congo. The southernmost large river generally included is the Shiloango. The region between the Shiloango and the Congo mouth is currently considered a transition zone, the fish fauna of which needs to be reviewed. Also for this region, a recent two-volume comprehensive work exists (Stiassny *et al.* 2007). This province has the highest number of families (47) and harbours 577 species, more than half of which are endemic (Stiassny & Hopkins 2007). The fact that the guide books do not present a final state of affairs for this province as well can be testified by the discovery of a new catfish genus (Friel & Vigliotta 2008) and two new *Doumea* catfish species in the Lower Guinea Province (Ferraris *et al.*, 2010).

Of special interest are the Cameroonese crater lakes, several of which harbour small endemic cichlid species flocks, as a result of sympatric speciation (Schliewen *et al.* 1994; Mc Gregor Reid & Gibson 2011). It has become clear that also for these unique fish communities, the basic taxonomic work is far from complete (e.g. Dunz & Schliewen 2010; Neumann *et al.* 2011; Bitja Nyom *et al.* 2012).

THE CONGO

The Congo is a basin of superlatives, being the largest and most species-rich river system of Africa, only second in the world after the Amazon. The basin includes some of the lakes of the East African rift valley, i.e. Kivu and Tanganyika, though from an ichthyogeographical point of view, Lake Kivu is part of the East Coast Province (Snoeks *et al.* 1997). The total number of described species (including the Tanganyika and Malagarasi systems) is about 1,250 (Snoeks *et al.* 2011), but many areas are underexplored and several hundreds of species are still awaiting description.

Traditionally, the basin has been split into three sub-basins, the Upper, Central and Lower Congo, with respectively the Boyoma or Wagenia rapids just upstream from Kisangani and the rapids at the outflow of the Pool Malebo near Kinshasa and Brazzaville acting as the two boundaries between the sub-basins. Lake Tanganyika is the oldest of the large African

lakes and harbours some 250 endemic cichlid species (Snoeks 2000), at least several tens of them still to be described. Even excluding the Lake Tanganyika endemics, about three quarters of the Congo species are estimated to be endemic.

After a long period of low activity, the exploration of the basin has intensified over the last decade. Recent activities are manifold and an overview is outside the scope of this chapter. A few interesting facts however illustrate the poor knowledge of, and the taxonomic confusion within the Congo fauna. For example, Ibala-Zamba (2010) found some 140 species in the lower reaches of the Léfini, a right bank affluent of the Middle Congo of which virtually nothing was known. If this is extrapolated to the enormous quantity of tributaries still to be explored, one gets an idea about the challenges facing us. Most progress has recently been made in the Lower Congo and surrounding areas, where several teams have worked, resulting in substantial changes of supposedly taxonomically stable groups and in the discovery of new evolutionary pathways in the highly specialized fauna (e.g. Hanssens 2009; Markert *et al.* 2010; Schwarzer *et al.* 2011; Lowenstein *et al.* 2011)

THE QUANZA

This province is probably the least explored African region. It includes the coastal rivers south of the Congo and north of the Cunene. Similar to the Congo region, political issues have hampered the study of these fishes in the past. The name of the province is derived from the largest basin in the region, the Quanza (Cuanza). However, the headwaters of this basin harbour a fish fauna that has clear affinities with the Zambezian fauna and hence should be included in this province (Scott 2005; Musilova *et al.* 2012; Skelton, pers. comm.). This observation has yet to be adopted in the ichthyogeographic literature of African freshwater fishes.

Much of the knowledge on the ichthyofauna of this province dates back to studies of Poll (1967). He listed 109 fish species, probably representing only a fraction of the real diversity of fishes, which has been very poorly sampled. One only has to look at the fish species richness map of southern Africa, resulting from the recent IUCN red list assessments (fig. 3.4 in Tweddle *et al.* 2009) to visually appraise the atypical disruption in species numbers between the species-rich Congo basin (not on the map) and the species-

rich areas (Cunene, Quanza headwaters) to the south and south east of the Quanza Province.

THE ZAMBEZI

The Zambezi Province includes the large Zambezi basin, the Indian Ocean coastal rivers south of the Zambezi past the Pongola to north of the Tugela River (Skelton 1994), the endorheic Okavango basin and the Cunene on the Atlantic coast. Lake Malawi also belongs to this province, though the lake is singled out because of its unique endemic species flock of 800 or more cichlid species, making it the species richest lake in the world (Snoeks 2004).

Skelton (2001) mentioned 178 species from the Zambezi Province but excluding the Lake Malawi basin, which is a surprisingly low number in view of the size of its main river and its complex geological history. Almost half of the species were estimated to be endemic to the province. The majority of these species (160) have been discussed by Marshall (2011) in a more than welcome major account to the fishes of Zimbabwe.

THE SOUTHERN OR CAPE PROVINCE

This province includes the whole southern part of Africa, south of the Zambezi province. It is probably the best-studied region on the African continent, though recent molecular studies clearly point at a serious underestimation of its species diversity (Skelton & Swartz 2011). It has a unique but very species-poor fauna with 36 species, all endemic, belonging to only four families with more than three quarters being cyprinids (Skelton 2001).

THE EAST COAST

This region includes the coastal rivers north of the Zambezi towards just south of the Juba River in Somalia; it also includes a major part of the African rift valley region including the catchment areas of lakes Kivu, Edward-George and Victoria-Kyoga (Snoeks *et al.* 1997). Together these lakes account for more than six hundred endemic haplochromine cichlids (Witte *et al.* 2009), several hundreds of which remain undescribed. Large parts of the Mozambican and Tanzanian coastal rivers remain underexplored. The last overview of the fish diversity of the province, but limited to the coastal river systems, was given

by Skelton (1994). He listed a modest number of 125 species with an estimated endemicity of about 60%. Typical for the region is the large radiation of the so-called annual killifish of the genus *Nothobranchius* and the relatively large number of endemic species of the tilapiine genus *Oreochromis*. Recent additions to the knowledge of fishes of the province include a study of the Rukwa fauna by Seegers (1996) and various studies on Lake Victoria mainly co-ordinated by the late Frans Witte, including the description of some new cichlid species (e.g. de Zeeuw *et al.* 2010).

MADAGASCAR

The Malagasy region, including Madagascar and its neighbouring islands, represent the most distinctive province of the Afrotropical region; it harbours an endemic fauna not found on the African main continent. Indeed all the species reported to live only in freshwaters, listed by Stiassny & Raminosoa (1994), are endemic. Primary freshwater fishes, such as Cyprinidae, Alestidae, Mochokidae, etc. are lacking. The number of endemic species is highest for the Cichlidae (with five endemic genera) and the endemic family Bedotiidae. Interestingly, the Madagascan representatives of a number of families (Cichlidae, Anchariidae, Mugilidae and Bedotiidae) represent basal taxa (Stiassny & Raminosoa 1994). A total of 135 native species (including undescribed ones) has been recorded from freshwater habitats, 90 of which are endemic to the province (Sparks & Stiassny 2005). Despite its uniqueness, the ichthyofauna of this region is highly threatened. Indeed the presence of many exotic species combined with habitat degradation through the loss of forests appears to result in a complete eradication of most native species (Stiassny & Raminosoa 1994).

CURRENT AND FUTURE CHALLENGES IN THE STUDY OF THE AFRICAN FRESHWATER FISH DIVERSITY

Morphology-based revisions often have broader implications that clearly go beyond the taxonomic domain. One such example is the revision of the African representatives of the cyprinid genus *Garra* studied by Getahun (2000). While seriously reshuffling the species accounts, the results also prompted a re-evaluation of the distribution and evolutionary history of the group. As a consequence, the Ethiopian rivers are

now known as the geographical centre of *Garra* diversity in Africa. Indeed, of the 18 species present in Africa, 12 occur in Ethiopia, six of which are endemic (Stiassny & Getahun 2007; Habteselassie *et al.* 2010). In addition, a seventh endemic new species has been found (Getahun & Snoeks, in prep.). Prior to Getahun's study (2000) only 11 African species were considered valid. Of these, two were found to be synonyms and three other species in synonymy needed to be resurrected (Stiassny & Getahun 2007). Therefore, it is fair to say that at that time, *Garra* taxonomy was in a neglected state and the notion of the north eastern part of Africa as a hotspot for *Garra* diversity has only developed after the results of the revision became available. Indeed, at present it is obvious that the major part (12 species at least) are endemic to Ethiopia and the surrounding region, while only a minority of species have distributions in western, central and eastern Africa.

While in the above discussions, attention has been drawn to certain under-explored areas and poorly studied faunas, one should not forget about the less obvious challenges that are still out there.

The African pike revision is one of the best recent cases in point, and reveals a story about a false feeling of confidence in groups perceived as taxonomically stable. For a long time indeed, the Hepsetidae was considered to be a monogeneric and monospecific family, widespread over Africa. The sole species *Hepsetus odoe* was easily identifiable even by non-specialists, so no taxonomic problem was envisaged. It was only after specimens with a relatively narrow head and some with a much broader head were found in the same river system (Vreven, pers. obs.), that the taxonomic alarm bell started to ring. Much to the surprise of the ichthyological community, a pan-African revision resulted in six clearly diagnosable species, the (re)descriptions of some of which are already published (Zengaya *et al.* 2011; Decru *et al.* 2012, 2013). Similarly, the revision of the electric catfish genus *Malapterurus* that traditionally was supposed to be either monotypic or to include two or three species, one of which very wide-spread, revealed an unexpected richness of 19 species currently considered valid, belonging to two different genera (Roberts 2000; Norris 2002; see also below).

Not all revisions plunge into the great (taxonomic) unknown. Some taxa remain remarkably stable and a recent study of Citharinidae, though bringing up interesting results (Moelants *et al.*, in prep.) did con-firm the taxonomy of the group as it largely has been for a century now.

As ichthyologists dig deeper in the complexity of African fish diversity, a multidisciplinary approach may offer many advantages. While this is on-going in studies of a variety of fish groups, maybe the best examples come from recent studies on Mormyridae, the weakly electric elephant fishes, in which morphological studies are combined with genetics and/or analyses of the electric organ discharges (e.g. Feulner *et al.* 2005; Lavoué *et al.* 2008; Kramer *et al.* 2012). Genetic studies, including barcoding, are also valuable tools to elucidate the validity of species and to uncover cryptic species (e.g. Lowenstein *et al.* 2011; Day *et al.* 2013; Pinton *et al.* 2013). However, one should not imply from the discovery of cryptic species that morphology-based taxonomy has failed in some particular cases. To a large extent, species will just remain cryptic, not because they are so hard to diagnose, but just because of a lack of an in-depth morphometric revision (which nowadays also translates as 'a lack of time by trained fish taxonomists to do the job'), as is illustrated in the *Hepsetus* case above. It is surprizing how little attention often is paid to the variable 'size' in comparisons between closely similar taxa. In fishes, the eye becomes relatively smaller with size; this negative allometry is usually linked to a positive allometry in the structures surrounding the eye on the head. In addition, the head itself can show allometry. The growth of fins can also be allometric (with sexual dimorphism in some groups as an extra confounding factor). Because of the continuous growth of fishes, in contrast to birds and mammals, and the limited number of specimens available, comparison of samples often needs to be done on specimens of different size classes. Though species are often diagnosed on characters that are assumed to be allometric, a decent discussion of the possible interference of this allometry in distinguishing between two taxa is often lacking, while simple scatterplots of the original or derived variables against a measure of size such as standard length already can give a first good insight. The lack of taking allometry into account might considerable complicate the identification of certain taxa, or even worse, cast doubt on the validity of the species.

A question (in a pragmatic sense) that comes up regularly is where geographical variation ends and species distinction starts. While this could be reduced to the traditional splitter versus lumper debate, it is more complex and becomes more and more an issue now that larger collections from various areas become available for study and further multivariate data analyses. While this problem pertains to riverine species as well, some good examples can be found among the cichlids from the lakes (Hanssens & Snoeks 2003; Risch & Snoeks 2008). In the endemic Lake Tanganyika cichlids such as *Tropheus*, morphology, genetic markers and colour pattern may present geographic variation, but not necessarily concordant, complicating species delineation (Van Steenberge, pers. comm.). In addition, differences between populations may occur without a geographical pattern, at least on the genetic level in Lake Malawi cichlids (Anseeuw *et al.* 2008).

More and more evidence accumulates demonstrating that hybridization is not the extremely rare event in African freshwater fishes as traditionally acknowledged. If such hybridisation events went beyond the phase of the odd hybrid individual (e.g. Decru *et al.* 2013), they can seriously hamper taxonomic studies (e.g. Vreven & Snoeks 2009). Old (in geological terms) hybridization events and introgression can be at the origin of new species (e.g. Salzburger *et al.* 2002 for an example in lamprologines of Lake Tanganyika). Therefore, the message is clear. Hybrids do occur and their presence in the samples studied has to be taken into account.

We conclude with an example illustrating how recent taxonomic studies can have a large input on ichthyogeographical assumptions. Greenwood (1983) ended his account on the zoogeography of African freshwater fishes with a list of examples of species (*Malapterurus electricus, Schilbe mystus, Heterobranchus longifilis, Hydrocynus vittatus, Alestes imberi, Alestes macrolepidotus, Hepsetus odoe, Barbus paludinosus*) with a distribution that spanned the majority of the provinces of the African continent. Currently, not much is left of this list. The distribution of *M. electricus* is now limited to the Nilo-Sudan and Upper Guinea and the former species has been split in various new taxa (Roberts 2000; Norris 2002). What used to be called *S. mystus* is now *S. intermedius* (De Vos 1995) and *S. mystus* is now regarded as essentially a Nilo-Sudan and Upper and Lower Guinea species. *Hydrocynus vittatus* is now considered as a complex, representing four genotype clades, the taxonomic status of which still needs to be addressed (Goodier *et al.* 2011). Two preliminary studies in the Royal Museum for Central Africa have shown that *A. imberi*, as currently defined, is clearly polyspecific while *A. macrolepidotus* represents a complex of species (Vreven, pers. comm.). The case of *H. odoe* has been discussed above. Finally, the distribution of *B. paludinosus* is much more restricted and the species is no longer considered to be present in western Africa nor in the Lower Guinea province (Skelton 2001). This leaves *H. longifilis* as the only species without a significant change in taxonomy or distribution from Greenwood's list. May more unknowns become known in the near future to deal with the clear need for better data on the taxonomy and distribution of African fresh and brackish water fishes.

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