Spawning migrations of the endemic *Labeobarbus* (Cyprinidae, Teleostei) species of Lake Tana, Ethiopia: status and threats

W. Anteneh*, A. Getahun†‡, E. Dejen§, F. A. Sibbing∥,

*Bahir Dar University, College of Science, Department of Biology, P. O. Box 79, Bahir Dar, Ethiopia,
†Addis Ababa University, Faculty of Life Sciences, Zoological Sciences Program Unit, P. O. Box 1176, Addis Ababa, Ethiopia,
§FAO Sub-Regional Office for Eastern Africa, P. O. Box 5536, Addis Ababa, Ethiopia,
∥Wageningen University, Experimental Zoology Group, P. O. Box 338, 6700 AH Wageningen, The Netherlands,
¶Wageningen University, Aquaculture and Fisheries Group, P. O. Box 338, 6700 AH Wageningen, The Netherlands,
**Institute for Marine Resources and Ecosystem Studies (IMARES), Wageningen UR, Haringkade 1, 1970 AB IJmuiden, The Netherlands,
††Fish for All, Addis Ababa, Ethiopia,
‡‡Netherlands Institute of Ecology (NIOO-KNAW), Department of Aquatic Ecology, P. O. Box 50, 6700 AB Wageningen, The Netherlands and
§§Institute for Marine Resources and Ecosystem Studies (IMARES), Wageningen Aquaculture, Wageningen UR, Korringaweg 5, 4401 NT Yerseke, The Netherlands

The reproductive biology of the only known intact species flock of large cyprinids, the 16 *Labeobarbus* species of Lake Tana (Ethiopia), has been extensively studied for the past two decades. Seven species of *Labeobarbus* are known to migrate >50 km upstream into tributary rivers for spawning during the rainy season (July to October), whereas eight other species are absent from these rivers and probably developed a new strategy of lacustrine spawning (macro-spatial segregation). One species (*L. intermedius*) probably spawns in the lake as well as in the rivers. Between the early 1990s and 2000s, the riverine spawners showed a decline of 75% in both biomass and number in both fishery independent surveys and in commercial catches. Reproductive migration makes fishes vulnerable to fishery and other threats like habitat modifications. Lacustrine spawners are probably more resilient as they are not known to form spawning aggregations that can easily be exploited by fishermen. In addition, upstream rivers and catchments around Lake Tana are highly degraded by erosion and recently subjected to intensive habitat modification for irrigation and hydroelectric power generation. This article reviews results of field studies on the *Labeobarbus* spawning migration from Lake Tana to spawning rivers, giving emphasis on segregation and homing. It also summarizes existing and emerging threats which form potential causes for the decline of the migratory *Labeobarbus* species. Knowledge gaps on the reproductive biology are identified for further investigation.

© 2012 The Authors
Journal of Fish Biology © 2012 The Fisheries Society of the British Isles

Key words: conservation; homing; large cyprinids; reproductive segregation; riverine spawning migration; species flock.

‡Author to whom correspondence should be addressed. Tel.: +2 51 911 11 9656; email: abebe12002@yahoo.com; abebeg@bio.aau.edu.et
∥Wageningen Aquaculture is a consortium of IMARES (Institute for Marine Resources & Ecosystem Studies) and AFI (Aquaculture and Fisheries Group, Wageningen University), both part of Wageningen University & Research Centre (WUR).

750 © 2012 The Authors
INTRODUCTION

Lake Tana (located at 12° N; 37° E and 1800 m altitude) is situated on the basaltic plateau of the north-western highlands of Ethiopia covering an area of c. 3050 km². It is the source of the Blue Nile River (Great Abbay), with a catchment area of c. 16 500 km² (Rzóska, 1976). Seven permanent rivers as well as c. 60 small seasonal rivers feed the lake. The main tributaries to the lake are Gilgel Abbay (Little Blue Nile), Megech, Ribb, Gumara, Dirma, Arno-Garno and Gelda Rivers (Fig. 1). Together they contribute >95% of the total annual inflow (Lamb et al., 2007). The Blue Nile is the only outflowing river. The shallow lake (average depth 8 m, maximum depth 14 m) is Ethiopia’s largest lake, containing half of the country’s freshwater resources, and is the third largest lake in the Nile Basin.

The water balance of Lake Tana was investigated by Setegn et al. (2008) on the basis of empirical measurements and simulations from 1978 to 2004. They estimated that 51% of the water input is by direct rainfall over the lake and only 44% by inflow from rivers. This relatively small contribution by inflowing rivers is the result of the relatively small catchment area as compared to the lake area. The water residence time is c. 3 years.

The climate is typical of semi-arid regions close to the equator, with a high diurnal temperature variation between day time extremes of 30° C to night lows of 6° C. For a tropical lake, Lake Tana has relatively low water temperatures (Dejen et al., 2004), varying between 20 and 27° C). Rainfall may reach up to 2000 mm year⁻¹ falling in one rainy season from June to October with one peak during July to September. Water levels are highest at the end of the rainy season and during the post-rainy period, slowly decreasing to a minimum around the end of the dry season. During October to June, evaporation exceeds input via rainfall and during this time many of the inflowing streams dry up completely (Alemayehu et al., 2010). Timing and amplitudes of rains have become increasingly unpredictable over the last decade (Minale & Rao, 2011).

The decadal trend analysis of Lake Tana water level and rainfall for the last 42 years (1965–2007) showed a negative slope for the last decade (1997–2007) (Minale & Rao, 2011). The lowest lake level was recorded during the time that water from the lake was taken for hydroelectric production in 2003. The slope for temperature in the last decade, however, was positive. Thus, recent decline in the level of Lake Tana was related to changes of climate and human influence (Minale & Rao, 2011). Consequently, these changes will have a negative effect on the fauna and flora in the lake.

Twenty of the 28 fish species of Lake Tana are endemic to the Lake Tana catchment (Getahun & Dejen, 2012). This high degree of endemism probably evolved because the incipient lake offered new habitats for adaptive radiation (Sibbing et al., 1998). The gene pool maintained its isolation from the lower Blue Nile basin by the 40 m high Tissisat Falls, 30 km downstream from the Blue Nile outflow.

Four fish families occur in Lake Tana (Nagelkerke, 1997). The Balitoridae, Cichlidae and Clariidae are represented by only one species each, Afronemacheilus abyssinicus (Boulenger, 1902), Oreochromis niloticus tana Seyoum & Kornfield 1992 and Clarias gariepinus (Burchell 1822). In contrast to the headwater lakes of the White Nile where haplochromine cichlids dominate, the fish fauna of Lake Tana is dominated by the family Cyprinidae, represented by four genera, i.e. Varicorhinus (one species, Varicorhinus beso Rüppell, 1836), Labeobarbus, Barbus and Garra.
Fig. 1. Lake Tana, (a) major inflowing rivers (river; road) and (b) planned water resource developments on the inflowing rivers (hydropower stations; major towns; main rivers; potential irrigation schemes; Tana catchment boundary). From Palstra et al. (2004) (a) and McCartney et al. (2010) (b).
Each of the last three genera developed new endemic species in Lake Tana (Nagelkerke, 1997; Nagelkerke & Sibbing, 2000; Stiassny & Getahun, 2007).

Lake Tana harbours 16 large (maximum 100 cm fork length, $L_F$) hexaploid labeobarbs (Labeobarbus spp.), which belong to a unique species flock of endemic cyprinids (Nagelkerke & Sibbing, 2000) (Fig. 2). Despite the overwhelming abundance of cyprinid fishes throughout the world’s freshwater systems, the Labeobarbus species of Lake Tana form, as far as is known, the only remaining intact species flock of large cyprinids in the world (Nagelkerke et al., 1994), since the one in Lake Lanao in the Philippines has practically disappeared due to anthropogenic activities (Kornfield & Carpenter, 1984). The species occupy different habitats as characterized by water depths and substratum types (Nagelkerke et al., 1994; de Graaf et al., 2008). Surprisingly, eight of the Labeobarbus species are piscivores (Sibbing & Nagelkerke, 2001; de Graaf et al., 2008). The only non-endemic labeobarb species present, the polymorph shore complex of Labeobarbus intermedius

Fig. 2. Lake Tana’s endemic Labeobarbus species flock (from de Graaf et al., 2004). Labeobarbus intermedius SC belongs to the polymorph shore complex (SC) of Lake Tana and probably is ancestral to the derived species of the flock.
(Rüppell 1835), is probably ancestral to this *Labeobarbus* species flock and a riverine generalist (Sibbing et al., 1998) that can be found throughout Ethiopia, in lakes and rivers (Banister, 1973).

In sharp contrast to *O. n. tana* and *C. gariepinus*, the *Labeobarbus* species are predicted to be by far the most susceptible to depletion by fisheries as the latter have a relatively short spawning period of 2 months year$^{-1}$, are predominantly riverine spawners, have a relative old age at maturity of 3–4 years (Wudneh, 1998), form spawning aggregations (Nagelkerke & Sibbing, 1996; Palstra et al., 2004; de Graaf et al., 2005; Anteneh et al., 2008) and are predominantly ecologically highly specialized endemics (Sibbing & Nagelkerke, 2001; de Graaf et al., 2008). The susceptibility of large African cyprinids to overexploitation has been proven repeatedly in the previous century, as attested by the collapse of *Labeo mesops* Günther 1868 fisheries in Lake Malawi (Skelton et al., 1991), *Labeo victorianus* Boulenger 1901 and *Barbus altianalis* Baulenger 1900 in Lake Victoria (Ogutu-Ohwayo, 1990) and *Labeo altivelis* Peter 1852 in Lake Mweru (Gordon, 2003).

For centuries, fishing on Lake Tana was executed by a reed-boat fishery, but after the introduction of a commercial motorized gillnet fishery in the late 1980s, fishing pressure increased progressively (de Graaf et al., 2006). The commercial gillnet fishery on *Labeobarbus* species is highly seasonal and mainly targets the spawning aggregations, as $>50\%$ of the annual catch is obtained from the river mouths during August and September (de Graaf et al., 2006). Village people living along the permanent rivers were also known to poison the spawning stocks using the crushed seeds of the birbira tree *Milletia ferruginea* (Nagelkerke & Sibbing, 1996).

Recruitment overfishing is hypothesized to be the most likely cause for the drastic decrease in abundance by c. 75% of the migratory riverine spawning *Labeobarbus* species and the collapse of juvenile *Labeobarbus* (between 5 and 18 cm $L_F$) by 90% during the 1990s (Wudneh, 1998; de Graaf et al., 2004, 2006). *Labeobarbus* catch per unit effort (CPUE) dropped from an average of 28 kg per trip in 2001 to 6 kg per trip between July and December 2010 (Mohammed et al., 2012). Some of the *Labeobarbus* spp. have become so rare that they have already been listed as endangered species by the International Union for Conservation of Nature (IUCN).

Most African labeobarbs occur in rivers and spawn there; the few known lake-dwelling species are considered to be riverine spawners as well (Skelton et al., 1991). In Lake Tana, seven of the 16 species are migratory and spawn in the permanent rivers. Gumara River and its tributaries is an important breeding ground (Alekseyev et al., 1996; Nagelkerke & Sibbing, 1996; Dgebuadze et al., 1999; Palstra et al., 2004), but not all rivers have been investigated yet. The labeobarbs aggregate at the river mouths and migrate upstream to spawn in shallow gravel beds, in fast flowing, oxygenated and clear small rivers (Palstra et al., 2004; Getahun et al., 2008). de Graaf et al. (2005) demonstrated that these species do not show spatial segregation among inflowing rivers but significant temporal segregation occurs in aggregating at the river mouths and in migrating towards the upstream spawning areas during the main rainy season (July to October). This migratory behaviour makes these species vulnerable to a number of threats. A serious threat to the migrating *Labeobarbus* populations may be the erosion of river banks due to poor land management practices (Setegn et al., 2009; Atnafu et al., 2011).

A final blow to the survival of riverine spawning *Labeobarbus* species could be the irrigation dams planned in most of the major rivers and the expected negative effects
on Lake Tana’s water level (McCartney et al., 2010) [Fig. 1(b)]. The main potential water quality effect arising from the construction and operation of dams are the high suspended solids concentrations resulting from construction activities or from operation of the dams, e.g. from pulses of sediment arising if the reservoir is operated with intermittent high flows to scour sediment from the reservoir bottom. The irrigation dam that is currently under construction in the Ribb River, for instance, is located in the middle of Labeobarbus spawning grounds. An irrigation dam (Getahun et al., 2008) will cause the loss of spawning habitat upstream from the dam, will reduce water flow over the dam during the spawning season and will prevent sufficient inundation of spawning areas downstream from the dam preventing successful reproduction. An integrated research programme for the Lake Tana basin is urgently required to prevent the collapse of an important fishery and the extinction of the only known large cyprinid species flock in the world.

This paper reviews results of field studies on Labeobarbus spawning migration from Lake Tana to their spawning rivers, giving emphasis on segregation and homing. It also summarizes the existing and emerging threats, potential causes for the decline of the migratory Labeobarbus species. Knowledge gaps on the reproductive biology are identified for further investigation.

**REPRODUCTIVE MIGRATION**

**ENVIRONMENTAL CUES**

Fishes use various environmental cues and internal stimuli for initiating migratory movement prior to spawning (Northcote, 1969; Raymond, 1979). A recent study of two Barbus species in the Lake Chilwa basin (Malawi) showed that river flow rate, conductivity and total suspended solids were significant predictors of the migration dynamics and reproductive status of the two barbs (Jamu et al., 2003).

Adult riverine spawning Labeobarbus migrate from the foraging area in the lake to the river mouths and most of them form pre-spawning aggregations (Palstra et al., 2004; de Graaf et al., 2005). Chemo-physical gradients may guide them to the river mouths. Increased lake water level, high turbidity (Palstra et al., 2004; de Graaf et al., 2005) and change in wind direction may serve as cues to trigger pre-spawning migration. Fluctuations in turbidity and silt inflow from the rivers are closely related with the water level (Rakowitz & Kubecka, 2006). The Lake Tana area has a tropical highland monsoon climate (Nagelkerke, 1997; Minale & Rao, 2011). The climate is strictly seasonal and dominated by the dry season (Bega; October until May) and a rainy season (Kiremt; June to October) with maximum rainfall in July. The dry season, however, is in some years interrupted by a small rainy season (Belg) in March (Wudneh, 1998; Anteneh et al., 2008). Even though the volume and turbidity of the tributaries may then increase slightly Labeobarbus do not form pre-spawning aggregations in March (de Graaf et al., 2005). This implies that either there is a threshold value of turbidity and water volume to trigger Labeobarbus migration or other environmental cues, such as changes in atmospheric conditions in the Lake Tana area that may trigger migration. Another possibility is that the fishes are not receptive to triggering cues at this time of the year, for instance, because of a less advanced reproductive status.
REPRODUCTIVE HOMING

It is generally accepted that some specific odorant variables of natal streams are imprinted on the olfactory system of juvenile salmonids during downstream drift and the adults evoke these factors to identify their natal stream in upstream spawning migration (Ueda et al., 2007; Hino et al., 2009). Unlike olfactory organs of terrestrial animals, only few chemicals, such as amino acids, steroids, bile acids and prostaglandins, elicit response from fish olfactory organs (Hara, 1994). For sockeye Oncorhynchus nerka (Walbaum 1792) and masu Oncorhynchus masou (Brevoort 1856) salmon in Lake Toya (Japan), it is found that dissolved free amino acids (DFAA) serve as natal stream odours (Ueda, 2011).

Although studies giving evidence for reproductive homing of Labeobarbus species in Lake Tana are absent, Palstra et al. (2004) hypothesized that homing might have facilitated and accelerated reproductive isolation, as in salmonids. The assumption is that the Labeobarbus species are monophyletic and the founder population of the riverine ancestral Labeobarbus used homing to spawn in specific streams. Hence, prior to the last desiccation of Lake Tana, 15 000 years ago (Lamb et al., 2007), reproductively segregated subpopulations could already have evolved. Fishes that exhibit homing migration use a follow up of triggers to find their spawning grounds (Ueda, 2011). In the case of Lake Tana Labeobarbus, these triggers may be the increased turbid inflow of river water into the lake, increased lake volume, decrease of water levels to swim upstream (Palstra et al., 2004), the imprinted smell of odorants (most probably DFAA) of the tributary spawning grounds and the pheromones of conspecifics (Zworykin et al., 2006; Ueda, 2011). The last two will induce final maturation and ovulation and as such specify the spawning ground as the migratory Lake Tana Labeobarbus were only found running on the spawning ground (Palstra et al., 2004).

Homing precision is high for salmonids; 100% for brown trout Salmo trutta L. 1758 (Stuart, 1957), whereas only 20% for a non-salmonid, muskelunge Esox masquinongy Mitchell 1824 (Crossman, 1990). Reproductive homing precision among the Lake Tana’s Labeobarbus may nowadays also be challenged as the catchment has undergone dramatic changes due to anthropogenic factors and climate irregularities (Minale & Rao, 2011). A poor precision (straying) could have strategic fitness value, especially where the natal spawning places are unsuitable during reproductive migration or when they are unstable and unpredictable (Lucas & Baras, 2001). Quantifying the precision of homing to natal spawning areas is very difficult in many freshwater fish species since the offspring may move away from the spawning grounds early in life and at a small size (Lucas & Baras, 2001). This is also true for the migrating labeobarbs in Lake Tana, as the juveniles swim from spawning streams to the pools of larger rivers (Anteneh et al., 2011). An alternative means to identify the presence of homing and to measure homing precision in riverine spawning labeobarbs is by examining repeated migration into spawning streams, possibly through electronic tagging or by testing olfactory discrimination of the possible odorants such as DFAA of streams through laboratory experiments.

SPAWNING MIGRATION PATTERNS AMONG LABEOBARBUS

The most intriguing and unique aspect of the reproductive biology of the Lake Tana Labeobarbus is that half of these species were not observed migrating upstream rivers
Table I. Overview of Lake Tana *Labeobarbus* species spawning strategies, spawning season and spawning rivers. Note that lacustrine spawners do not aggregate at the river mouths. (Sources: Palstra *et al*., 2004; de Graaf *et al*., 2005; Anteneh *et al*., 2007, 2008)

<table>
<thead>
<tr>
<th>Species</th>
<th>Reproductive strategy</th>
<th>Spawning season</th>
<th>River mouth for spawning aggregation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. macrophthalmus</em></td>
<td>Riverine</td>
<td>Post rainy</td>
<td>Gumara†, Ribb, Gelgel Abbay, Gelda</td>
</tr>
<tr>
<td><em>L. truttiformis</em></td>
<td>Riverine</td>
<td>Rainy</td>
<td>Gumara†, Ribb, GelgelAbbay, Gelda,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Megech†, Dirma†</td>
</tr>
<tr>
<td><em>L. megastoma</em></td>
<td>Riverine</td>
<td>Rainy</td>
<td>Gumara†, Ribb, GelgelAbbay, Gelda,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Megech†, Dirma†</td>
</tr>
<tr>
<td><em>L. brevicephalus</em></td>
<td>Riverine</td>
<td>Post rainy</td>
<td>Gumara†, Ribb, GelgelAbbay, Gelda,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Megech†, Dirma†</td>
</tr>
<tr>
<td><em>L. tsanensis</em></td>
<td>Riverine</td>
<td>Rainy</td>
<td>Gumara†, Ribb, GelgelAbbay, Gelda,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Megech†, Dirma†</td>
</tr>
<tr>
<td><em>L. platydorsus</em></td>
<td>Riverine</td>
<td>Rainy</td>
<td>Gumara†, Ribb, GelgelAbbay, Gelda,</td>
</tr>
<tr>
<td><em>L. acutirostris</em></td>
<td>Riverine</td>
<td>Rainy</td>
<td>Gumara†, Ribb, GelgelAbbay, Gelda,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Megech†, Dirma†</td>
</tr>
<tr>
<td><em>L. intermedius</em></td>
<td>Lacustrine*</td>
<td>Year round</td>
<td>Gumara†, Ribb, GelgelAbbay, Gelda,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Megech†, Dirma†</td>
</tr>
<tr>
<td><em>L. nedgia</em></td>
<td>Lacustrine*</td>
<td>Rainy</td>
<td>Do not aggregate</td>
</tr>
<tr>
<td><em>L. dainelli</em></td>
<td>Lacustrine</td>
<td>Rainy</td>
<td>Do not aggregate</td>
</tr>
<tr>
<td><em>L. gorguari</em></td>
<td>Lacustrine</td>
<td>Rainy</td>
<td>Do not aggregate</td>
</tr>
<tr>
<td><em>L. longissimus</em></td>
<td>Lacustrine</td>
<td>Rainy</td>
<td>Do not aggregate</td>
</tr>
<tr>
<td><em>L. gorgorensis</em></td>
<td>Lacustrine</td>
<td>Rainy</td>
<td>Do not aggregate</td>
</tr>
<tr>
<td><em>L. surkis</em></td>
<td>Lacustrine</td>
<td>Post rainy</td>
<td>Do not aggregate</td>
</tr>
<tr>
<td><em>L. crassibarbis</em></td>
<td>Lacustrine</td>
<td>Rainy</td>
<td>Do not aggregate</td>
</tr>
<tr>
<td><em>L. ossensis</em></td>
<td>Lacustrine</td>
<td>Rainy</td>
<td>Do not aggregate</td>
</tr>
</tbody>
</table>


†Collected in the river mouth and its upstream area.

to spawn (Table I). Such species seem to have successfully adapted to the lacustrine environment and probably complete their whole life cycle, including reproduction, inside the lake (de Graaf *et al*., 2005). Lacustrine spawning would be a novel derived strategy and probably evolved to avoid spending energy on migration and be able to spawn multiple times per year in more stable lake habitats. Therefore, for littoral species, lake spawning could be a profitable and adaptive phenomenon. Evidence for particular spawning grounds in the lake remains unknown. Some fragmentary observations are documented to indicate the presence of lacustrine spawning. In October 1995, one male and one female running *Labeobarbus dainellii* (Bini 1940) were collected from the littoral zone of Lake Tana on the west side of the Bahir Dar Gulf, very close to the town and far from any of the known spawning rivers (Nagelkerke & Sibbing, 1996). Ripe *Labeobarbus intermedius* (Rüppell 1835) were found throughout the year, and for *Labeobarbus surkis* (Rüppell 1835) from November to January (Nagelkerke & Sibbing, 1996; de Graaf *et al*., 2005). The missing *Labeobarbus* species most likely also spawn in the lake and adjacent floodplains. Lacustrine spawners may have developed strategies that make their developing eggs and larvae less dependent on circulating oxygen that seems crucial for successful development of the offspring of riverine spawners. Lacustrine spawners may deposit their eggs on sand or rocks, near roots of plants or on aquatic or flooded terrestrial
Fig. 3. *Labeobarbus* species composition (*⩾*, *L. brevicephalus*; *⪗*, *L. macrophthalmus*; *⪖*, *L. truttiformis*; *⪕*, *L. tsanensis*; *⪔*, *L. acutirostris*; *⪙*, *L. megastoma*; *⪈*, *L. platydorsus*; *⪗*, *L. intermedius* SC; *⪘*, Others) of the overnight gillnet settings as a function of (a) geographic location (i.e. in four different river mouths) during July to October breeding period and (b) time (i.e. in four different months) in the river mouths (from de Graaf et al., 2005). *n*, number of fishes; *N*, number of gillnet settings. Note the similarity of species composition between the (a) different river mouths and (b) changes in species composition over the breeding period.

vegetation as is common in many other cyprinid genera (Mills, 1991). Using the littoral vegetation or rocky shores or both as spawning sites will provide both shelter from predators and high densities of prey for larvae and juveniles.

Spawning migration of *Labeobarbus* of Lake Tana can be partitioned into three stages (Palstra et al., 2004): (1) migration from the foraging area in the lake to the river mouth (pre-spawning aggregation), (2) ascending upstream the river’s main channel and (3) entering a tributary for spawning (except those species which are assumed to be spawning in the main channel). Sexual differences in aggregation profile and the exact period the aggregating fishes spend at the river mouths before swimming upstream is not clearly known. From gonado-somatic indices and abundance data, however, they probably spend days or weeks aggregating at the river mouths (de Graaf et al., 2005). This pre-spawning aggregation at the river mouths might improve the synchronization of individual gonad cycles (Whitehead, 1959) of the widely dispersed Lake Tana labeobarbs. Most probably, *Labeobarbus megastoma* (Nagelkerke & Sibbing 1997) swims directly to the rivers’ main channels without pre-spawning aggregation. Although it is a common phenomenon, migration of fishes need not involve their aggregation in high concentration (Lucas & Baras, 2001).

*Labeobarbus* spawning migration into the main channels of the rivers occurs mostly after the peak of the heavy rainy season (Nagelkerke & Sibbing, 1996; Wudneh, 1998; Dgebuadze et al., 1999; Palstra et al., 2004; Anteneh et al., 2008), when flow rate and average water level decrease. Since the riverine spawning labeobarbs migrate >50–60 km in the Ribb River main channel within a few days (Getahun et al., 2008), the energetic costs will be high if upstream swimming occurs during...
SPAWNING MIGRATIONS OF LAKE TANA *LABEOBARBUS* 759

high flow rates. Spawning migration of *Labeobarbus* finally ends in the small tributary streams of rivers. Dgebuaze *et al.* (1999) and Palstra *et al.* (2004) reported that in Gumara River, riverine spawning labeobarbs enter into small tributaries such as Dukolit, Kizen and Wanzuma in the evening, spawn overnight and return to the main channel with first light. In the Lake Tana area, rains mostly start in the late afternoon and cause a fast rise in the small tributaries. Their water level falls in the following morning. This late afternoon rain may trigger nocturnal spawning (Palstra *et al.*, 2004).

REPRODUCTIVE SEGREGATION

Spatio-temporal segregation

Macro-spatial segregation in spawning was observed between lake and river spawners. Meso-spatial spawning segregation, e.g. each species of migratory riverine spawning *Labeobarbus* choosing its own river (Gumara, Ribb, Gelda, Megech, Dirma, Arno-Garno or Gelgel Abbay River), for spawning was rejected by de Graaf *et al.* (2005) [Fig 3(a)]. Studies in some streams of Gumara (Palstra *et al.*, 2004) and Megech (Anteneh *et al.*, 2008) indicated micro-spatial spawning segregation (Table II). In the tributaries of Ribb River, micro-spatial segregation was not found (Getahun *et al.*, 2008; Table II). *Labeobarbus brevicephalus* (Nagelkerke & Sibbing 1997) and *Labeobarbus tsanensis* (Nagelkerke & Sibbing 1997) were consistently present at all spawning tributaries studied so far. Similarly, except in Wanzuma and Wombha, *Labeobarbus truttiformis* (Nagelkerke & Sibbing 1997) was also widely distributed in the spawning tributaries except in Gumara tributaries where it only dominated in Kizen (Table II).

The absence of *L. intermedius* in Gumara River (Palstra *et al.*, 2004; Table II) is confusing, since it was one of the most abundant species in all other streams of tributary rivers. *Labeobarbus intermedius* remains quite abundant at the river mouths throughout the year, but its catch during the rainy season is significantly higher (de Graaf *et al.*, 2005).

Except *L. intermedius* which spawns throughout the year (de Graaf *et al.*, 2005; Anteneh *et al.*, 2007), the migratory riverine spawning *Labeobarbus* species do not aggregate simultaneously at the river mouths (de Graaf *et al.*, 2005). Although there is considerable overlap, the shift in species abundance in the weekly catch at the spawning streams clearly showed a trend of temporal segregation [Fig. 3(b)]. Seven species showed significant temporal segregation while aggregating at the river mouths. Similarly, in migrating towards the upstream spawning areas (Palstra *et al.*, 2004; Getahun *et al.*, 2008), they revealed temporal segregation (Fig. 4). Most labeobarbs are abundant and with running gonads from mid-August until mid-October.

Size-dependent assortative mating (Nagel & Schluter, 1998; Schliewen *et al.*, 2001) may possibly isolate the spawning species since the $L_f$ at 50% maturity ($L_{F50}$) values differ highly among these different riverine spawning labeobarbs (de Graaf *et al.*, 2003). Micro-spatial and temporal segregations (Palstra *et al.*, 2004) and smell (Zworykin *et al.*, 2006) are also thought to isolate spawning labeobarbs. Sexual dimorphism which is common among African cichlid species (Seehausen & van Alphen, 1998), however, is absent among *Labeobarbus* species (Dgebuadze *et al.*, 1999).

© 2012 The Authors
<table>
<thead>
<tr>
<th>Species</th>
<th>Gumara (Palstra et al., 2004)</th>
<th>Ribb River (Getahun et al., 2008)</th>
<th>Megech (Anteneh et al., 2008)</th>
<th>Arno-Garno (Gebremedhin, 2011)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Kizen</td>
<td>Wanzuma</td>
<td>Dukolit</td>
<td>Chibirna</td>
</tr>
<tr>
<td>L. acutirostris</td>
<td>4</td>
<td>11</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>L. brevicephalus</td>
<td>271</td>
<td>230</td>
<td>318</td>
<td>101</td>
</tr>
<tr>
<td>L. macrophthalmus</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>L. intermedius</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>36</td>
</tr>
<tr>
<td>L. megastoma</td>
<td>6</td>
<td>3</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>L. truttiformis</td>
<td>26</td>
<td>0</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>L. tsanensis</td>
<td>129</td>
<td>110</td>
<td>325</td>
<td>3</td>
</tr>
<tr>
<td>L. nedgia</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>6</td>
</tr>
</tbody>
</table>
Fig. 4. Temporal segregation among Labeobarbus species in (a) the Gumara (Palstra et al., 2004) and (b) Megech and Dirma Rivers (Anteneh et al., 2008). Catch collected from the main channels as well as from streams. CPUE, the number of specific Labeobarbus per hour, respectively, per trap or per fyke net (in Gumara River), but in Megech and Dirma Rivers, it is defined as the number of fish per overnight gillnet setting. Note the CPUE scale differences for different species.

PERSPECTIVES OF APPLYING MODERN FISH MIGRATION STUDY METHODS IN LABEOBARBUS SPECIES FLOCK

Despite extensive research, using traditional methods, on the spawning migrations of labeobarb species throughout the lake and its tributary rivers since mid 1990s (Alekseyev et al., 1996; Nagelkerke & Sibbing, 1996; Dgebuadze et al., 1999; Palstra et al., 2004; de Graaf et al., 2005; Anteneh et al., 2008; Getahun et al., 2008; Gebremedhin, 2011), the exact timing of each labeobarb species to aggregate at the river mouths and enter into the rivers and then their migration to actual spawning in small tributaries and the exact location of the spawning areas of each species is
not yet completely resolved. Eight of the 15 *Labeobarbus* species are totally missing from the tributary rivers. Although these missing species are assumed to be lacustrine spawners (de Graaf *et al.*, 2005), no information is available about their spawning grounds. Even among the riverine spawners such as *L. brevicephalus*, clear and convincing data about their reproductive spatial segregation are lacking. Morphological resemblances of the labeobarb species, the lake’s large area (>3000 km²) and turbidity as well as large size of some tributary rivers during labeobarb spawning (rainy) season preclude visual detection of migrants. Therefore, the use of state-of-the-art methods, such as radio-tracking, molecular markers, otolith microchemistry, underwater remote sensing (using acoustics) and geographic information system (GIS), could provide more insight in the mechanism regulating the migration and reproduction of Lake Tana’s labeobars.

Lake Tana is located in the highlands of Ethiopia, is source of the Blue Nile and is inhabited by the only known intact species flock in the world of large cyprinids: 16 *Labeobarbus* species. Field studies on the endemic *Labeobarbus* species flock of Lake Tana show macro-spatial segregation in spawning between seven riverine spawners and eight species that may have developed a derived strategy, lake spawning. The ancestral species *L. intermedius* uses both strategies. The river spawners migrate (1) from the lake to the river mouth for aggregation and probably synchronize maturation, (2) migrate up the rivers to the spawning streams and (3) migrate into the small streams for actual spawning. Not all species are bound to specific rivers, although for some micro-segregation in time and space over the spawning streams is observed. Mechanisms of reproductive segregation and homing need further study and radio-tracking, otolith microchemistry, microsatellites and *I*G are highly recommended. Cues that trigger migration in the rainy season (June to October) are not clear yet, although both water level and turbidity of lake and its tributaries are likely. Wind and other atmospheric conditions may also contribute as triggers, an area to investigate. Lake spawning is adaptive and profitable since it extends the spawning season and area, avoiding high costs for migration. River spawning and especially migration make labeobars more sensitive to fishery pressure. Major threats to recruitment of future stocks are recruitment overfishing at the river mouths and on the spawning grounds as well as traditional toxifying practices. Land degradation has adverse effects on water quality in spawning streams. Federal and regional legislation has been approved but due to lack of proper implementation, they did not deter the drastic decline of labeobarb catches from 40% in 1990 towards 15% in 2010. Current and emerging threats involve the construction of dams and reservoirs on the labeobarb spawning grounds, which undermine the ecological values and functions of the Lake Tana ecosystem. Mitigation measures are urgently recommended to integrate ecological and economical values of the system. An integrated assessment of hydrology, ecology and livelihoods is required.

References


© 2012 The Authors


**Electronic References**

