



Influence of irrigation infrastructures and water quality on fish assemblages in Lake Tana tributaries, north-west Ethiopia

Gizachew Teshome · Abebe Getahun ·
Minwelet Mingist · Glenn Wilson ·
Wassie Anteneh

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Abstract Lake Tana is one of East Africa’s largest freshwater bodies, yet many of its fishes are migratory and utilize in-flowing tributaries as critical spawning habitat. However, factors such as expanding water resources developments and sand mining along these rivers and streams may disrupt this ecosystem function. We monitored juvenile and adult fish abundance and water quality across five lake tributaries from August 2014 to April 2015 to examine how irrigation schemes and water quality affect assemblage and population structure. Adult assemblages were dominated by *Labeobarbus* cyprinids and varied between tributaries, albeit without separation by irrigation development or sand mining. Overall, adult abundances of the dominant migratory *Labeobarbus* species were four-fold higher below the Shini River irrigation weir than upstream. Contrastingly, juvenile abundances were often significantly higher above these structures. Juvenile abundances decreased on average by 46% along the first 1000 m of two irrigation canals, suggesting poor habitat

suitability or high mortalities from water withdrawals. Water quality varied more between rivers than sampling times, but without any separation of tributaries by irrigation or sand mining. Conductivity and turbidity-related parameters had the highest correlation with adult assemblage structure and individual species abundances. These findings indicate that Lake Tana tributaries must be managed on a case by case basis, with more focus given to mechanisms allowing fish to bypass irrigation developments and the direct assessment of fish populations between sand mining and other sites.

Keywords Fish assemblage · Rivers · Weirs · Aquatic habitat management

Introduction

Lakes hold nearly 90% of the world’s liquid freshwater resources and represent a key ecosystem for aquatic

G. Teshome
Department of Biology, College of Natural and Computational Sciences, University of Gondar, P.O. Box 196, Gondar, Ethiopia

G. Teshome (✉) · A. Getahun
Department of Zoological Sciences, College of Natural and Computational Sciences, Addis Ababa University, P.O. Box 1176, Addis Ababa, Ethiopia
e-mail: gizachew2006@gmail.com

M. Mingist
Department of Fisheries and Aquatic Sciences, School of Fisheries and Wildlife, College of Agriculture and Environmental Sciences,

Bahir Dar University, P.O. Box 79, Bahir Dar, Ethiopia

G. Wilson
Department of Biology, University of Southern Denmark, Campusvej 55, Dk 5230 Odense-M, Denmark

W. Anteneh
Department of Biology, College of Science, Bahir Dar University, P.O. Box 79, Bahir Dar, Ethiopia

biodiversity (Duker and Borre 2001). Indeed, their relatively isolated nature means that they frequently harbour high levels of aquatic species endemism (Martens and Segers 2009). Lake Tana is one of the largest lakes in East Africa (over 3000 km²) and in the top 32 for conservation priority for Africa and 250 globally (Duker and Borre 2001). It was registered as a UNESCO biosphere reserve in 2015 due to its ecological, religious and socioeconomic importance (Worku 2017). However, in line with many developing tropical regions, the Lake Tana basin is under severe stress from high human population growth and the associated need for increased energy, food and potable water security (Karlberg et al. 2015; Mequanent and Mingist 2019), placing substantial pressure on aquatic ecosystem integrity and biodiversity (Dudgeon et al. 2006).

An estimated 28 fish species inhabit Lake Tana (Getahun and Dejen 2012), including 21 that are endemic to Ethiopia and the last remaining cyprinid (*Labeobarbus*) species flock globally (Nagelkerke et al. 1994). A number of these species are now registered on the IUCN Red List with assessments ranging from Data Deficient to Endangered. Beyond their biodiversity value, Lake Tana's *Labeobarbus* and other fishes contribute substantially to local fishers' income and household protein although their populations have declined by over 90% since the early 1990s (de Graaf et al. 2004, 2006; Tesfaye and Wolff 2014; Dejen et al. 2017). Despite Lake Tana's size, its tributaries play a disproportionately large role in shaping the population ecology of the resident fishes, and the most critical threats to species recovery are believed to be those occurring within these tributary environments. Lake Tana is fed by more than 40 small seasonal and seven larger perennial tributaries, although the Blue Nile River is its only outflow (Vijverberg et al. 2009). Quantifying the impact of key threats to fishes during their tributary residency is essential in an attempt to rebuild population strength.

Flow alteration is a key threatening process for riverine ecosystems (Poff et al. 1997). The resulting shifts in flow timing, volume and duration, and the ways in which the associated infrastructures are designed and operated, may have a wide range of ecological consequences (Bunn and Arthington 2002). These can include drying or decline of stream flow and reduced connectivity (Jackson and Marmulla 2001), loss of cues to upstream migration (Thorstad et al. 2007) or time of spawning (Nessler et al. 1988; King et al. 1998),

restricted access to floodplain or other nursery habitats (Junk et al. 1989; Kingsford 2000; Humphries et al. 2006), thermal depression and a disconnection between the timing of spawning and peaks in availability of larval prey (Humphries et al. 2013; Rolls et al. 2013), or reduced capacity for downstream larval or juvenile dispersal (O'Connor et al. 2006). A plethora of varying-sized dams along Lake Tana's tributaries are thought to have caused major disruptions to spawning migration routes, and water withdrawals for upstream irrigation have increased the frequency and duration of cease-to-flow events around the slope and lowland spawning reaches (MoWR 2010; Anteneh et al. 2012; Dejen et al. 2017; Gebremedhin et al. 2017).

Excessive instream sedimentation is also a major challenge for aquatic ecosystems in the Lake Tana basin. Riparian erosion is widespread across most of the region (Steenhuis et al. 2014; Abate et al. 2017), and sand mining in the river channel is expanding along many of the lake's tributaries (Mingist and Gebremedhin, 2016). The effects of this are likely to be of particular significance to benthic-spawning species like *Labeobarbus*, including the filling in of deep pools and smothering of gravel beds by mobilized sediment, while the associated suspended material is known to lower the survival of pelagic early life-history stages in other species (Westerberger et al. 1996; Kjelland et al. 2015). Indirect effects may also result from raised levels of nutrients and organic matter and physicochemical parameters such as pH or salinity within the water column. Should such peaks occur during the spawning season, the implications for reproductive success (Sutherland 2007) or assemblage structure (Sutherland et al. 2002) may be substantial and add to those impacts already driven by impoundments.

The present study assessed patterns in the abundance of migratory adult and juvenile fishes across five tributaries of Lake Tana from August 2014 to April 2015. We used a mix of multivariate and univariate approaches to (a) examine how assemblage structure varied over time and between tributaries with and without irrigation dams and in-channel sand mining, (b) directly assess how irrigation infrastructure (dams, diversion canals) influences adult and juvenile abundances, and (c) determine which physicochemical water characteristics are most associated with adult assemblage structure and species abundance within these river systems. Although impacts of weirs on upstream spawning migration have been previously inferred in nearby rivers (e.g.

Gebremedhin et al. 2017), we included analyses of adult abundances upstream and downstream of one such weir as a partial reference for the potential impacts on assemblage structure within our study rivers and at the time of our fieldwork. The parallel effects on juvenile abundances, and whether weirs or lowered water quality may be linked to variation in assemblage structure, remain poorly understood for the region.

Materials and methods

Study area

Lake Tana is located at an elevation of approximately 1790 m above sea level, with an estimated surface area of 3050–3600 km² and a catchment area of approximately 16,500 km² (Vijverberg et al. 2009). The region's climate is dominated by a wet season between July and September and a dry season from December to April (Dejen et al. 2017). We selected five tributaries along a 48 km length of the lake's eastern shoreline, namely the Qimon, Arno, Shini, Chibirma and Guanta rivers (Fig. 1), based on the presence of water resources development works and in-channel sand mining. All have villages or small towns in their close vicinity, and small-scale fish harvesting along their length.

The Qimon River (ca. 22 km) flows directly into Lake Tana, and currently has no in-channel irrigation structures or sand mining activities. The surrounding land uses are predominantly small-scale livestock and crop production. The Arno River (ca. 44 km) also flows directly into Lake Tana but has both irrigation infrastructure and sand mining activities within its channel. Numerous small irrigation diversion weirs are located up to 30 km from its mouth, with a typical headloss of around 1.8 m. Irrigation canals of 1–3 km in length take water withdrawals from above these weirs to small-scale irrigated cropping. Sand mining occurs predominately over a 10 km stretch of the river towards its upper end. Adjacent land use is predominantly small-scale irrigated cropping downstream and non-irrigated cropping and livestock grazing upstream.

The Shini River (ca. 49 km) is a tributary of the Ribb River, with their confluence 8.5 km upstream of the Ribb outflow into Lake Tana. It has both irrigation infrastructure and sand mining activities along its channel. Two irrigation weirs are located 33 and 37 km from its mouth, with a headloss of approximately 2.5 m and

irrigation canals of around 1.2 km in length conveying water to small-scale irrigated cropping. Sand mining occurs over approximately 12 km of the river from 7.5 km upstream of the mouth. The Chibirma River (ca. 20 km) is a tributary of the Shini River, with their confluence 7 km upstream of the Ribb River. It has neither in-channel sand mining nor irrigation weirs. Land use along both tributaries is predominantly small-scale irrigated and non-irrigated cropping and livestock grazing.

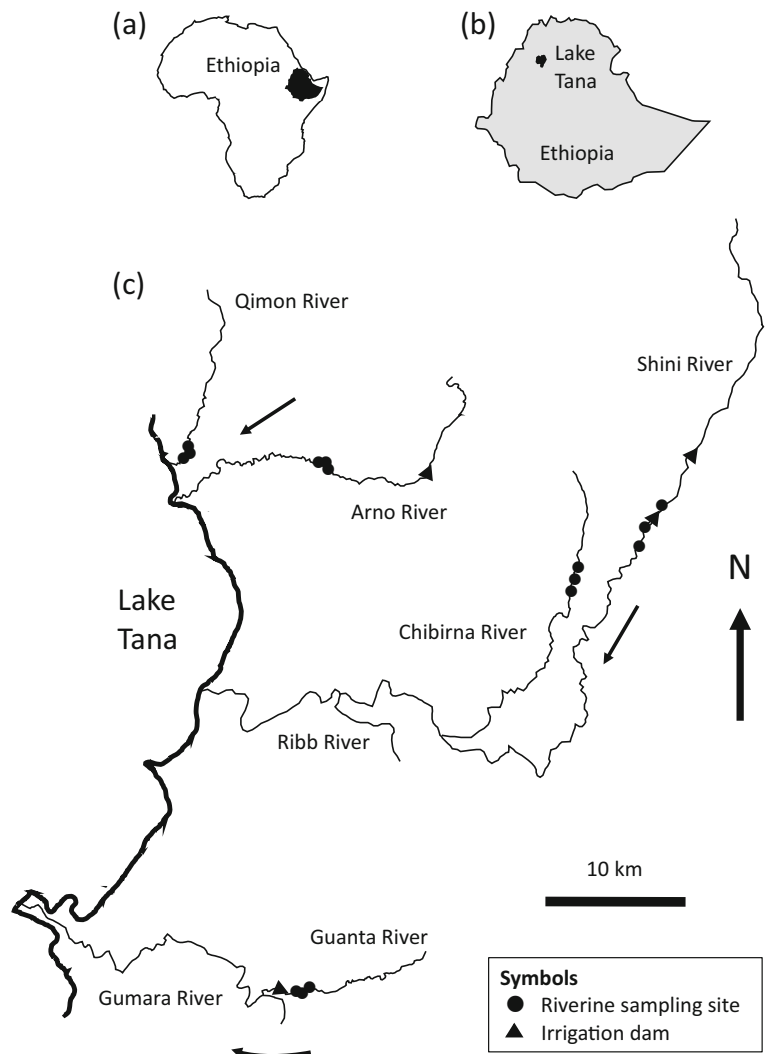
The Guanta River (ca. 19 km) is a tributary of the Gumara River, with its confluence 28 km upstream of the Gumara outflow. It has an irrigation weir located 4.3 km upstream of its confluence with the Gumara (3 m headloss). Adjacent land use is similar to that of the other rivers.

Field methods

Sampling of fish was done at approximately 30-day intervals from all tributaries on five occasions between August and November 2014, with two trips falling within September. Three sampling sites were selected along a 300 to 1900 m length of each tributary (Fig. 1c), based on ease of channel access, presence of a sufficient sampling area, and availability of expected spawning site characteristics such as sand or gravel beds. We used a combination of two multifilament gillnets with 6, 8, 10 and 12 cm stretched mesh panels and a single monofilament gillnet with 4 and 6 cm mesh panels, each net measuring 25 × 1.5 m. Sampling was limited to between 1000 and 1500 h due to the high evening flow rates following heavy afternoon rains. Multifilament gillnets were set for 4 h and monofilament gillnets were set for 2 h. In August and September 2014, we undertook additional adult fish sampling to compare adult abundances within 50 m upstream and downstream of the Shini River irrigation weir. This used the same sampling gears and soak times as per other adult sampling. For all adult fish sampling, fish were removed from the nets on the bank, identified to species (Nagelkerke and Sibbing 2000; Getahun and Dejen 2012), and their body length (standard length, fork length and total length, all in mm) and wet weight (g) recorded. In all cases, net soak duration was recorded and used to standardize catch per unit effort.

At the same time as each adult fish sampling, six physicochemical water quality parameters were measured: conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$), pH, temperature ($^{\circ}\text{C}$),

Fig. 1 Location of (a) Ethiopia in Africa, (b) Lake Tana, and (c) sampling locations along the five study tributaries. Arrows in (c) indicate the direction of flow. Note, the Ribb and Gumara rivers are only shown to slightly upstream of their study tributary confluences



dissolved oxygen ($\text{mg}\cdot\text{L}^{-1}$) and total dissolved solids (TDS, ppm) using Wagtech Int. portable water quality meters, and Secchi depth (cm) using a standard Secchi Disk.

Juveniles were sampled monthly along the Arno and Shini tributaries from December 2014 to February 2015 and again in April. This sampling period was selected as it spans the main irrigation season. No data were available for March 2015 as some canal sampling sites were dry. Sites were located from approximately 50 m downstream and 30 m upstream of the main irrigation weir on each tributary and within the irrigation canal within 50 m of the canal entrance (site 1 below). Juvenile abundances were also compared along the same irrigation canals, from the head of the canal (site 1) and then a further 500 and 1000 m downstream (sites 2 and 3,

respectively). All juvenile sampling used a combination of 25×2 m beach seine and 1.8×1.6 m mosquito nets with a mesh size of 5 and 2 mm, respectively. Three replicate hauls were taken with each net, along 100 m of the canal and tributary sites, around 20 to 35 m apart. At the upstream and downstream sampling sites, each net haul was 10 m^2 in area whereas they were either 7.5 m^2 (site 1) or 3.5 m^2 (sites 2 and 3) within the canals due to space limitations. Accordingly, juvenile abundance estimates were adjusted to a standardized sampling area of 10 m^2 (comparison of tributary sites with canal site 1) or 7.5 m^2 (comparison of canal sites 1–3). Apart from *L. beso*, *Labeobarbus* juveniles could not be identified any further over the size range encountered, although were easily distinguished from other juveniles including *Enteromius* species based on the identification key of

Anteneh et al. (2013). We also discriminated *Garra* juveniles from adults by their body shape and length. Accordingly, our juvenile data were grouped as either *L. beso*, remaining *Labeobarbus* species, or *Garra dembecha*, and also all species pooled.

Statistical analyses

Adult fish data were pooled within each tributary x sampling trip combination for final analyses. Non-metric multi-dimensional scaling (NMDS) ordination was first used to display patterns in assemblage structure between tributaries and the five sampling trips, based on the Bray-Curtis similarity resemblance matrix and fourth-root transformed data. One-way analysis of similarities (ANOSIM) was used to test for significant differences between tributary and sampling trip groups using the same similarity matrices, while similarity percentages (SIMPER) analysis was used to examine the relative contribution of individual species to any significant pair-wise comparison of tributaries or sampling trips.

The effect of the Shini River irrigation dam on total adult abundances of the four dominant migratory fishes (*Labeobarbus intermedius*, *L. beso*, *L. brevicephalus* and *L. nedgia*) was examined for August and September 2014 using simple frequency histograms. Variation in juvenile abundances was then examined between upstream and downstream of the Arno, Shini and Guanta River irrigation weirs and within each diversion canal entrance using two-way analyses of variance (ANOVA). These were performed separately for all species combined, *Labeobarbus* species combined (excluding *L. beso*), and both *L. beso* and *G. dembecha* on their own, with both Tributary and Site treated as fixed factors. Variation in juvenile abundances was also examined between the mouth and downstream sites along the Arno and Shini irrigation canals using two-way ANOVAs, with Tributary and Site again treated as fixed factors and separate analyses for the four datasets (all species combined, *Labeobarbus* species excluding *L. beso*, *L. beso*, *G. dembecha*). In both cases, the ANOVA was performed using $\log(x + 1)$ transformed data and the nature of any significant differences was determined using Tukey HSD post-hoc tests.

Patterns in water quality across the five tributaries and sampling trips were examined using metric multi-dimensional scaling ordination based on the Euclidian distance resemblance matrix and normalized $\log(x + 1)$ transformed data. ANOSIM was then used to test for significant differences between river and trip groups, based

on the same similarity matrices, and the variables most responsible for any significant pairwise comparisons were determined using SIMPER analyses.

BIO-ENV (Clarke and Gorley 2015) was used to investigate the influence of water quality variables on adult fish assemblage structure across the five tributaries and sampling trips. This employed Spearman Rank correlation coefficients to test for significant relationships between the adult fish abundance and water quality data matrices. Again, these were based on the Bray-Curtis similarity matrix of the fourth-root (fish) and Euclidean distance matrix of normalized $\log(x + 1)$ (water quality) datasets. BIO-ENV results were expressed as the best solution involving up to five water quality variables.

Significant associations between each water quality variable and adult fish abundance were tested using two-tailed Spearman Rank correlations for each of the six most abundant fish species across all tributaries and sampling trips. Due to the number of tests undertaken, significant relationships were accepted at $p \leq 0.10$ to reduce the risk of Type II errors.

All univariate analyses were performed using SPSS version 26, while multivariate analyses were undertaken using Primer version 7.0.13.

Results

Adult fish abundance, diversity and assemblage structure

A total of 1302 fish and 13 species were sampled over the five tributaries and five sampling trips (Table 1). These were dominated by *Labeobarbus* species (9 species, 95.5% of the total catch) while the remaining taxa comprised *Enteromius humilis*, *Clarias gariepinus*, *Garra dembecha* and *Oreochromis niloticus*. *Labeobarbus intermedius* and *L. brevicephalus* were the most abundant species (72.5% overall) and were encountered across all tributaries and on most sampling trips. *Labeobarbus nedgia* and *L. beso* were absent from just the Qimon River, while all remaining species were found in one to three tributaries. The total species count per tributary ranged from four in the Guanta to nine in those without in-channel dams or sand extraction (Chibirna and Qimon). Ten species and 407 fish were encountered during the first September trip

Table 1 Summary of adult fish abundance and diversity between the five study tributaries of Lake Tana, Ethiopia, and five sampling trips, August to November 2014

Tributary	Month	<i>Labeobarbus besu</i>	<i>L. brevicephalus</i>	<i>L. crassibarbis</i>	<i>L. degeni</i>	<i>L. intermedius</i>	<i>L. megastoma</i>			
Qimion	August		5	2		4				
	September 1		34			62				
	September 2		56			9				
	October		23			21	2			
	November		8			13	3			
	August		16	1		55				
	September 1		39			105				
	September 2	3	12			16				
	October		18			17				
	November	1	8			6				
Chibima	August	9	7			33				
	September 1	4	9		1	19				
	September 2	2	7			22				
	October	14	1			23				
	November	44				33				
	August	5	7			30				
	September 1	9	9		2	7				
	September 2	6	7			28				
	October	8	1			34				
	November	23				9				
Guanta	August					7				
	September 1	7	34			18				
	September 2	5	8			15				
	October		9			17				
	November	6	10			9				
	Total number	146	332	3	3	612	5			
	Percentage of total catch	11.21	25.50	0.23	0.23	47.01	0.38			
	Tributary	<i>L. nedgia</i>	<i>L. truttiformis</i>	<i>L. isanensis</i>	<i>Barbus humilis</i>	<i>Clarias gariepinus</i>	<i>Garra dembecha</i>	<i>Oreochromis niloticus</i>	Total number of fish	Number of species
	Qimion		2						11	3
	Arno							1	97	3
							2	67	3	
1					1		20	70	7	
			3				3	33	6	
6								78	4	

Table 1 (continued)

Tributary	<i>L. nedgia</i>	<i>L. truttiformis</i>	<i>L. isanensis</i>	<i>Barbus humilis</i>	<i>Clarias gariepinus</i>	<i>Garra dembecha</i>	<i>Oreochromis niloticus</i>	Total number of fish	Number of species
	9				2			155	4
	9							40	4
								35	2
								15	3
Chibirna	5							54	4
	6			1	6	1		47	8
	10			1	1		1	44	7
	4						1	43	5
	6						1	84	4
Shini	9							54	4
	15				5			47	5
	29							72	5
	16				2		1	61	5
	10				2		1	45	5
Guanta								10	2
								61	4
								28	3
		3						26	2
		2						25	3
Total number	135	10	3	2	19	1	31	1302	13
Percentage of total catch	10.37	0.77	0.23	0.15	1.46	0.08	2.38		

and either six or eight species and 202 to 251 fish during the remaining trips.

The NMDS of adult abundance data showed considerable variation in assemblage structure both within and between tributaries (Fig. 2a). ANOSIM detected significant differences among tributaries (Table 2, $p=0.001$) as well as between all but two of the tributary pairs: comparison of the Shini River with its Chibirna tributary and of the Qimon and Guanta rivers. No consistent separation of irrigation from non-irrigation tributaries was evident, nor of tributaries with in-channel sand mining from those without it. In contrast, no significant differences in adult assemblage structure were detected between sampling trips (Fig. 2b; Table 2).

SIMPER analysis indicated that most of the significant tributary comparisons were primarily driven by differences in the abundance of *L. nedgia*, *L. beso* and *L. brevicephalus* (Table 3). The single exception was variation between the Arno and Qimon rivers, which was mainly due to differences in *O. niloticus* and *L. nedgia* abundances. The level of dissimilarity between tributary pairs was highest for the Shini and Qimon (55.6%) and Chibirna and Qimon (52%) rivers and lowest for the Arno and Guanta rivers (35.7%).

Effect of irrigation infrastructure on adult fish

Adults of the four dominant *Labeobarbus* species in the Shini River were present in much higher abundances downstream than upstream of the sampled irrigation dam during August and September 2014 (Fig. 3). Overall, abundances below the dam were

Table 2 ANOSIM of variation in adult fish assemblage structure between the Lake Tana study tributaries and sampling trips, August to November 2014. ns, not significant at $\alpha=0.05$

Sample test	R	P	
Difference between Tributaries			
Global test	0.416	0.001	
Shini River v Chibirna River	-0.048	0.579	ns
Shini River v Arno River	0.432	0.008	
Shini River v Qimon River	0.912	0.008	
Chibirna River v Arno River	0.456	0.008	
Chibirna River v Qimon River	0.816	0.008	
Arno River v Qimon River	0.348	0.032	
Guanta River v Shini River	0.560	0.008	
Guanta River v Chibirna River	0.532	0.008	
Guanta River v Qimon River	0.188	0.103	ns
Guanta River v Arno River	0.108	0.032	
Difference between sampling trips			
Global test	-0.051	0.756	ns
Trip 1 v Trip 2	0.012	0.437	ns
Trip 1 v Trip 3	0.004	0.429	ns
Trip 1 v Trip 4	-0.016	0.508	ns
Trip 1 v Trip 5	-0.008	0.421	ns
Trip 2 v Trip 3	-0.108	0.690	ns
Trip 2 v Trip 4	-0.092	0.667	ns
Trip 2 v Trip 5	0.008	0.444	ns
Trip 3 v Trip 4	-0.088	0.659	ns
Trip 3 v Trip 5	-0.084	0.690	ns
Trip 4 v Trip 5	-0.064	0.579	ns

four-fold higher than upstream. *Labeobarbus intermedius* was the only species captured upstream

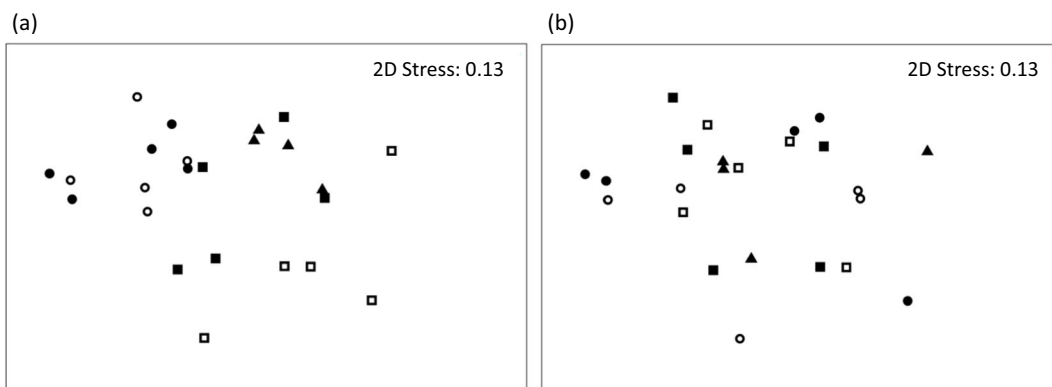


Fig. 2 Non-metric multi-dimensional scaling ordination of adult fish assemblage structure between (a) the Lake Tana study tributaries (● Shini, ○ Chibirna, ■ Arno, ◻ Qimon, ▲ Guanta) and (b) five sampling trips (▲ 1, ■ 2, ◻ 3, ● 4, ○ 5), August to November 2014

Table 3 SIMPER analysis of the contribution of individual fish species to differences in adult assemblage structure between the Lake Tana study tributaries, Ethiopia, August to November 2014. Comparisons are shown only for river pairs which differed significantly (ANOSIM, Table 2)

Species	Mean abundance	Cumulative %	%D	Species	Mean abundance	Cumulative %	%D
Shini River – Arno River							
	Shini	Arno	37.94	Arno River – Qimion River	Arno	Qimion	41.20
<i>Laabeobarbus beso</i>	1.73	0.46	23.32	<i>Oreochromis niloticus</i>	0.00	1.12	19.33
<i>Laabeobarbus nedgia</i>	1.96	1.01	42.73	<i>Laabeobarbus nedgia</i>	1.01	0.20	36.08
<i>Laabeobarbus brevicephalus</i>	1.05	2.02	60.91	<i>Laabeobarbus intermedius</i>	2.30	2.00	48.18
<i>Clarias gariepinus</i>	0.77	0.24	74.46	<i>Laabeobarbus truttiformis</i>	0.00	0.50	58.24
				<i>Laabeobarbus brevicephalus</i>	2.02	2.10	67.41
				<i>Laabeobarbus beso</i>	0.46	0.00	76.54
Shini River – Qimion River							
	Shini	Qimion	55.60	Guanta River – Shini River	Guanta	Shini	46.82
<i>Laabeobarbus nedgia</i>	1.96	0.20	21.56	<i>Laabeobarbus nedgia</i>	0.00	1.96	32.34
<i>Laabeobarbus beso</i>	1.73	0.00	42.38	<i>Laabeobarbus brevicephalus</i>	1.52	1.05	47.56
<i>Laabeobarbus brevicephalus</i>	1.05	2.10	56.12	<i>Laabeobarbus beso</i>	0.94	1.73	62.31
<i>Oreochromis niloticus</i>	0.40	1.12	65.99	<i>Clarias gariepinus</i>	0.00	0.77	75.06
<i>Clarias gariepinus</i>	0.77	0.20	74.87				
Chibirna River – Arno River							
	Chibirna	Arno	37.70	Guanta River – Chibirna River	Guanta	Chibirna	45.81
<i>Laabeobarbus beso</i>	1.77	0.46	24.40	<i>Laabeobarbus nedgia</i>	0.00	1.56	25.75
<i>Laabeobarbus brevicephalus</i>	1.20	2.02	39.78	<i>Laabeobarbus beso</i>	0.94	1.77	43.05
<i>Laabeobarbus nedgia</i>	1.56	1.01	54.35	<i>Laabeobarbus brevicephalus</i>	1.52	1.20	56.68
<i>Oreochromis niloticus</i>	0.60	0.00	65.55	<i>Oreochromis niloticus</i>	0.00	0.60	66.85
<i>Clarias gariepinus</i>	0.51	0.24	74.93	<i>Laabeobarbus truttiformis</i>	0.50	0.00	75.16
Chibirna River – Qimion River							
	Chibirna	Qimion	51.99	Guanta River – Arno River	Guanta	Arno	35.65
<i>Laabeobarbus beso</i>	1.77	0.00	22.66	<i>Laabeobarbus nedgia</i>	0.00	1.01	23.04
<i>Laabeobarbus nedgia</i>	1.56	0.20	40.24	<i>Laabeobarbus beso</i>	0.94	0.46	44.41
<i>Laabeobarbus brevicephalus</i>	1.20	2.10	52.59	<i>Laabeobarbus brevicephalus</i>	1.52	1.20	63.49
<i>Oreochromis niloticus</i>	0.60	1.12	61.58	<i>Laabeobarbus intermedius</i>	1.88	2.30	76.90
<i>Laabeobarbus truttiformis</i>	0.00	0.50	68.12				
<i>Laabeobarbus intermedius</i>	2.25	2.00	74.62				

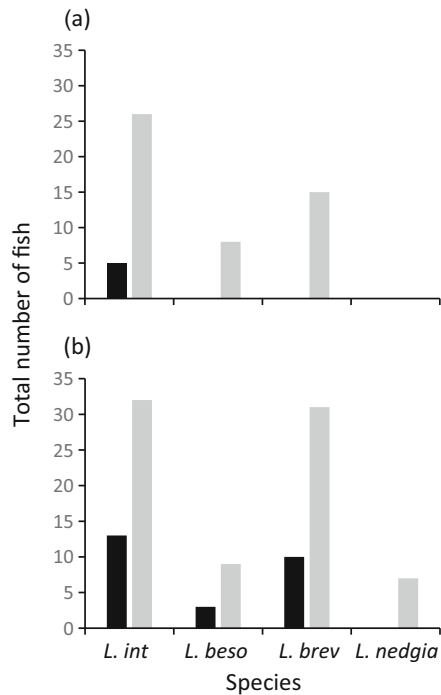


Fig. 3 Variation in abundance of the dominant migratory *Labeobarbus* species between upstream (black bars) and downstream (grey bars) of the Shini River irrigation dam, (a) August and (b) September 2014. *L. int*, *Labeobarbus intermedius*; *L. brev*, *Labeobarbus brevicephalus*. Data are the total number of each species sampled per site per month

of the dam in August, while *L. nedgia* was only encountered downstream in September.

Patterns in juvenile abundances

Juvenile abundances were generally highest in the Shini and Arno rivers and upstream of the irrigation weirs (Fig. 4; Table 4), although we detected a significant interaction between the effects of tributary and site for two of the data sets (all species pooled, *Labeobarbus* species pooled). In both cases, there was no difference in abundances between sites in the Arno River, but significantly higher abundances either upstream (Shini) or downstream (Guanta) of the irrigation weir. For *L. beso* on its own, abundances were significantly higher in the Arno and Shini rivers and upstream of the irrigation weir. While no significant site difference was detected for *G. dembecha* juveniles, their abundances were higher in the Arno and Shini rivers than in the Guanta.

Juvenile abundances did not show any statistical differences along the Arno and Shini irrigation canals for any of the four data sets (Fig. 5, Table 5). Nevertheless, mean abundances were consistently lower at site 3 for all four data sets and both canals, declining from sites 1 to 3 by an average of 46.4% (Fig. 5).

Variation in water quality and its influence on adult abundances

Variation in the six water quality parameters across the five tributaries is shown in Tables 6. When examined together, these indicated significant variation in the physicochemical characteristics among tributaries overall ($p = 0.001$) and between six of the 10 tributary pairs (Fig. 6a; Table 7). However, significant temporal variation was only evident between the first and final two sampling trips (Fig. 6b; Table 7). SIMPER analysis (Table 8) revealed that differences between tributaries and sampling trips were mostly driven by water temperature and the two parameters related to water turbidity (TDS, Secchi depth).

Water physicochemical characteristics appeared to explain some of the variability in adult assemblage structure across the study tributaries and sampling interval (Table 9). The variable most associated with these patterns was conductivity ($r_s = 0.398$ on its own). In combination with TDS, pH and Secchi depth, it explained almost 44% of the variation in assemblage structure. Similarly, the variables most associated with the abundances of individual species were conductivity and TDS (Table 10). Interestingly, these associations were all positive, indicating greater adult abundances under conditions of higher conductivity and turbidity levels.

Discussion

The diversity and uniqueness of Lake Tana's fishes have now been established for over 20 years, including the systematics and ecomorphological differentiation of members of the *Labeobarbus* species flock (Nagelkerke et al. 1994; Nagelkerke and Sibbing 2000) and how these sit within the broader assemblage (Getahun and Dejen 2012). However, we now also have a stronger sense of the main threats faced by these species, particularly in conjunction with their tributary habitat requirements and use. Findings from the present

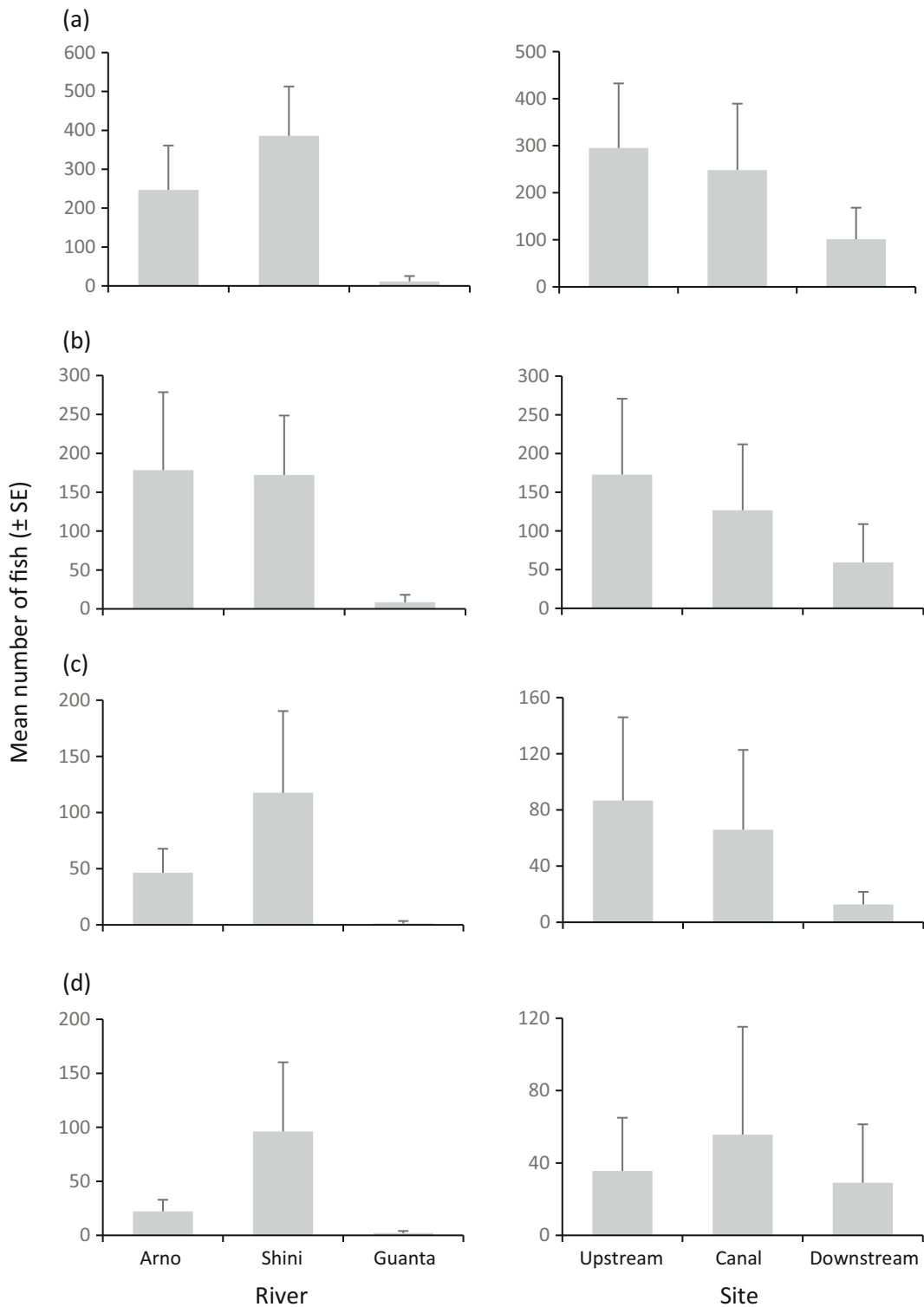


Fig. 4 Variation in mean juvenile abundance between sites upstream, downstream and within the irrigation canal of the Arno, Shini and Guanta rivers, December 2014 to April 2015. **(a)** All species combined, **(b)** *Labeobarbus* spp. excluding *L. beso*, **(c)**

L. beso, and **(d)** *Garra dembecha*. Variation between sites is shown separated by tributary for **(a)** and **(b)** due to a significant tributary x site interaction term (Table 4). Note varying y-axis scales. Data are shown ±1 standard error

Table 4 Summary of two-way ANOVA of mean juvenile abundance in the Arno, Shini and Guanta rivers and upstream, downstream and within each tributary's irrigation canal, December 2014 to April 2015. Significance levels: *, $p \leq 0.1$; **, $p \leq 0.01$; ***,

$p \leq 0.001$. Data were analysed as $\log(x + 1)$. An α value of 0.10 was used to reduce the likelihood of Type II errors although all tests were significant at $p \leq 0.05$. Sites: US, upstream; Ca, canal; DS, downstream

Test	Source	df	Mean square	F	Post-hoc comparisons	
All species combined	Model	8	4.665	9.730	***	
	Intercept	1	90.313	188.368	***	
	Tributary	2	13.117	27.358	***	Arno=Shini > Guanta
	Site	2	0.601	1.254		
	Tributary x Site	4	2.471	5.154	**	Arno: US=Ca=DS Shini: US=Ca>DS Guanta: US=Ca<DS
<i>Labeobarbus</i> spp. excluding <i>L. beso</i>	Model	8	3.683	9.270	***	
	Intercept	1	70.997	178.706	***	
	Tributary	2	9938	25.016	***	Arno=Shini > Guanta
	Site	2	0.550	1.386		
	Tributary x Site	4	2.121	5.340	**	Arno: US=Ca=DS Shini: US=Ca>DS Guanta: US=Ca<DS
<i>L. beso</i>	Model	8	2.745	6.955	***	
	Intercept	1	38,532	97.631	***	
	Tributary	2	7.928	20.088	***	Arno=Shini > Guanta
	Site	2	1.366	3.460	*	US=Ca, US > DS, Ca=DS
	Tributary x Site	4	0.843	2.135		
<i>Garra dembecha</i>	Model	8	1.960	4.455	**	
	Intercept	1	32.144	73.081	***	
	Tributary	2	5.484	12.467	***	Arno=Shini > Guanta
	Site	2	0.238	0.541		
	Tributary x Site	4	1.059	2.407		

study add to this understanding and demonstrate the effects of irrigation infrastructures on adult fish diversity and adult and juvenile abundances within Lake Tana tributaries, as well as how physicochemical water characteristics may shape adult assemblages and abundances.

Our findings particularly indicate the need for a stronger understanding of Lake Tana tributaries as individual fish biodiversity units. Most tributary pairs had a significantly different fish assemblage, and the prominence of tributary variation in physicochemical water characteristics further reinforces this notion. For *Labeobarbus* species, de Graaf et al. (2005) concluded that there were no species preferences for different tributaries, albeit from having only sampled around river mouths along the Lake Tana shoreline. For practical

reasons, past studies of Tana tributary fishes (present study included) have only examined a subset of the lake's tributaries, and some differences in interpreting patterns may have arisen from the choice of fishing methods or other aspects of the sampling design. Determining how assemblage structures vary across all Tana tributaries using past data and comparable metrics would help establish existing monitoring gaps as well as a stronger sense of any key threat hotspots from planned impoundments or other factors.

Instream barriers can play a role in structuring migrating tropical fish populations (Lorenzen et al. 2007), including across the present study region. We detected higher diversity and abundances of adult fish downstream than upstream of the Shini irrigation dam at the end of the 2014 wet season and onset of the

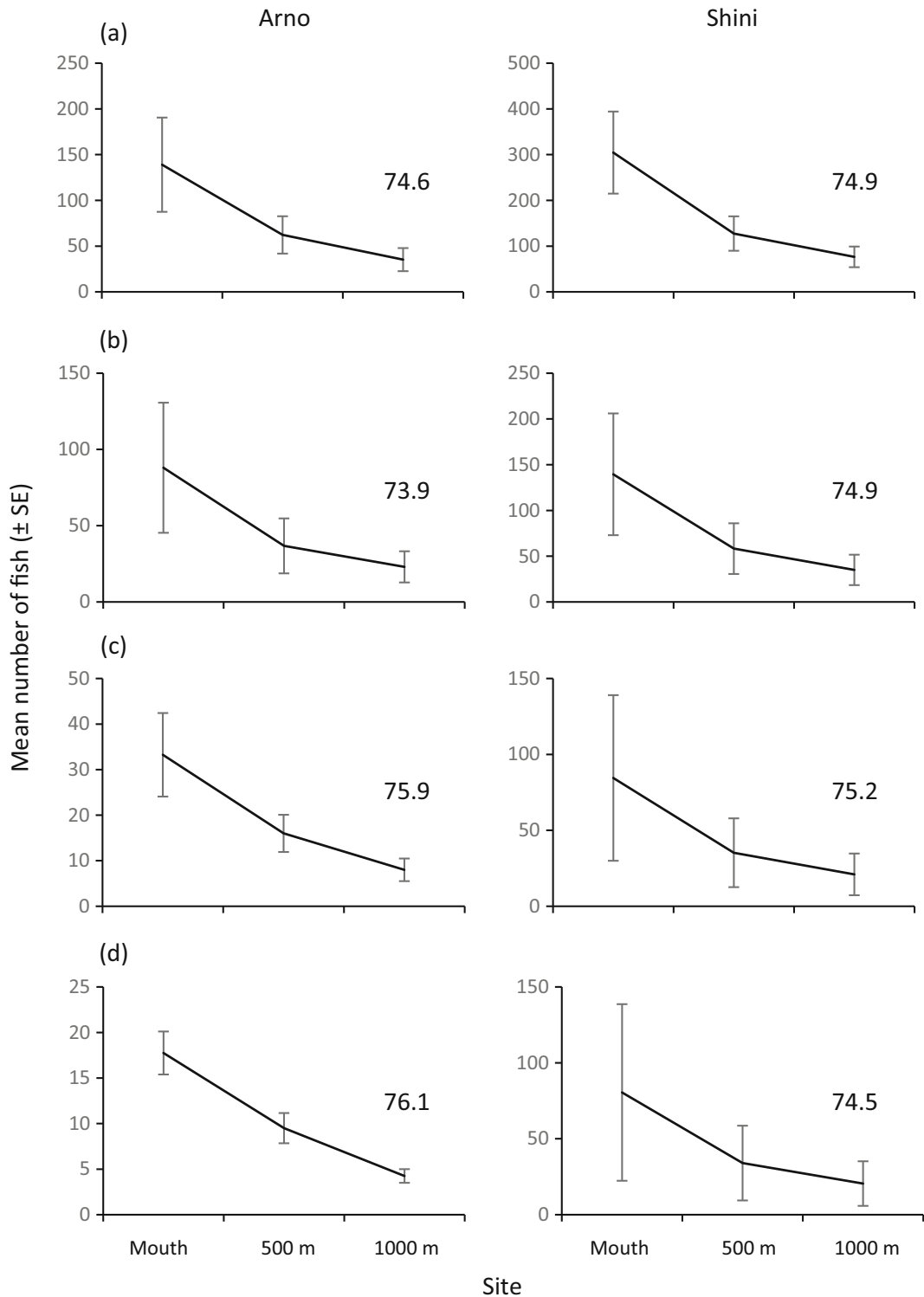


Fig. 5 Variation in mean juvenile abundance along the Arno River and Shini River irrigation canals, December 2014 to April 2015. **(a)** All species combined, **(b)** *Labeobarbus* spp. excluding *L. beso*, **(c)** *L. beso*, and **(d)** *Garra dembecha*. Numbers shown on

each graph indicate the mean percentage decline in abundance between the Mouth and 1000 m sites. Note varying y-axis scales. Data are shown ± 1 standard error

Table 5 Summary of two-way ANOVA of mean juvenile abundance along the Arno River and Shini River irrigation canals, December 2014 to April 2015. Significance level: ***, $p \leq$ 0.001. An α value of 0.10 was used to reduce the likelihood of Type II errors although all tests were significant at $p \leq 0.05$. Sites: 1, mouth; 2, 500 m; 3, 1000 m

Test	Source	df	Mean square	F	
All species combined	Model	5	0.153	0.948	
	Intercept	1	106.998	664.331	***
	Tributary	1	0.429	2.661	
	Site	2	0.166	1.033	
	Tributary x Site	2	0.001	0.007	
<i>Labeobarbus</i> spp. excluding <i>L. beso</i>	Model	5	0.097	0.683	
	Intercept	1	79.258	558.231	***
	Tributary	1	0.225	1.582	
	Site	2	0.128	0.902	
	Tributary x Site	2	0.001	0.014	
<i>L. beso</i>	Model	5	0.065	0.124	
	Intercept	1	44.225	83.914	***
	Tributary	1	0.005	0.010	
	Site	2	0.152	0.289	
	Tributary x Site	2	0.008	0.016	
<i>Garra dembecha</i>	Model	5	0.081	0.173	
	Intercept	1	36.969	78.401	***
	Tributary	1	0.076	0.161	
	Site	2	0.150	0.318	
	Tributary x Site	2	0.015	0.033	

Labeobarbus spawning season. Similarly, when Gebremedhin et al. (2017) compared assemblages between dam and non-dam Tana tributaries, they found significantly higher *Labeobarbus* diversity downstream of irrigation dams on two tributaries but not along two other undammed streams. Most of our 15 assemblage sampling sites were downstream of irrigation dams and this may have contributed to the lack of an irrigation signal in our NMDS and ANOSIM results for assemblage structure.

In contrast, however, we found a general pattern of juvenile entrainment *upstream* of the Arno and Shini irrigation dams. This is the first direct demonstration of irrigation dams appearing to hinder downstream fish movement in any East African river system. The capacity for juvenile downstream movement is critical in many fishes for subsequent growth and adult development (O'Connor et al. 2006) and has also been inferred from longitudinal abundance patterns in another Tana tributary, the Gelda River (Anteneh et al. 2011). Yet, juveniles may often be reluctant to navigate instream

barriers (Behrmann-Godel and Eckmann 2003) or else sustain lethal and sub-lethal injuries in the process (Bell and DeLacy 1972). Both factors could potentially lead to downstream recruitment deficits in river-spawning species. Improved weir designs (Haro et al. 1998) or options such as installing bypass channels around structures (Gebler 1998; Lorenzen et al. 2007) may help reduce such impediments. In situations where flow velocities can be adjusted to account for the swimming capabilities of small fish, doing so during critical migration points in the lunar or annual cycle may be a cheaper, more practical solution to boost recruitment downstream of existing structures. Unfortunately, Ethiopian instream barriers often have an inflexible, fixed-crest design (authors' personal observations), and solutions such as bypass channels may have greater efficacy.

Although we did not detect a statistically significant pattern in juvenile abundances along the Arno and Shini irrigation canals, there were nonetheless substantial numbers of juveniles within them and an average

Table 6 Variation in river water quality parameters between the five tributaries of Lake Tana, Ethiopia, August to November 2014. Data are presented as means ± 1 standard error

Tributary	Dissolved oxygen (mg.L ⁻¹)	Temperature (°C)	Conductivity (µS cm ⁻¹)	Total dissolved solids (ppm)	pH	Secchi Depth (cm)
Qimon River	6.75 ± 0.55	19.62 ± 0.20	222.82 ± 32.49	150.96 ± 22.66	8.49±0.21	70.40 ± 4.92
Arno River	7.22 ± 0.41	21.33 ± 0.64	191.56 ± 9.76	124.46 ± 8.05	8.19±0.22	65.60 ± 7.10
Chibirna River	6.44 ± 0.66	21.84 ± 0.69	289.02 ± 15.58	196.74 ± 9.76	8.11±0.15	78.42 ± 8.40
Shini River	6.77 ± 0.54	19.76 ± 0.29	246.66 ± 8.78	167.86 ± 6.19	8–07±0.09	79.60 ± 8.78
Guanta River	5.60 ± 0.53	21.82 ± 0.54	167.68 ± 16.17	113.28 ± 11.11	7.96±0.20	35.00 ± 8.37

reduction of around 46% in abundance between the canal entrance and 1000 m downstream. Whether irrigation canals represent a supportive habitat extension for Tana tributary juveniles and small fishes to any extent is unclear. However, there are two possible mechanisms underpinning the reduced abundances downstream. The first is that dispersal into canals is mostly limited to their upstream reaches. Roberts and Rahel (2008) found substantial movement by trout within a large canal system using radio-tracking.

Nevertheless, extensive entrainment and dispersal of fish have not always been evident along even large canal systems (Daniels 2001; although see King and O’Connor 2007). A radio-tracking or similar approach would be needed to gauge the extent to which varying dispersal rates were responsible for our patterns.

The second potential explanation, however, is declining habitat suitability downstream, particularly in terms of loss of water depth. Roberts and Rahel (2008) found a 77% mortality rate of their radio-tracked fish after flows

Table 7 ANOSIM of variation in water quality characteristics between the Lake Tana study tributaries and sampling trips, August to November 2014. ns, not significant at α = 0.05

Sample test	R	P	
<i>Difference between Tributaries</i>			
Global test	0.280	0.001	
Shini River v Chibirna River	0.324	0.032	
Shini River v Arno River	0.344	0.008	
Shini River v Qimon River	0.072	0.325	ns
Chibirna River v Arno River	0.400	0.008	
Chibirna River v Qimon River	0.280	0.056	ns
Arno River v Qimon River	0.080	0.286	ns
Guanta River v Shini River	0.520	0.008	
Guanta River v Chibirna River	0.440	0.024	
Guanta River v Qimon River	0.284	0.040	
Guanta River v Arno River	0.160	0.095	ns
<i>Difference between sampling trips</i>			
Global test	-0.001	0.474	ns
Trip 1 v Trip 2	0.052	0.286	ns
Trip 1 v Trip 3	0.014	0.127	ns
Trip 1 v Trip 4	0.268	0.016	
Trip 1 v Trip 5	0.228	0.040	
Trip 2 v Trip 3	-0.172	0.921	ns
Trip 2 v Trip 4	-0.196	0.905	ns
Trip 2 v Trip 5	-0.092	0.444	ns
Trip 3 v Trip 4	-0.204	1.000	ns
Trip 3 v Trip 5	-0.052	0.595	ns
Trip 4 v Trip 5	-0.056	0.659	ns

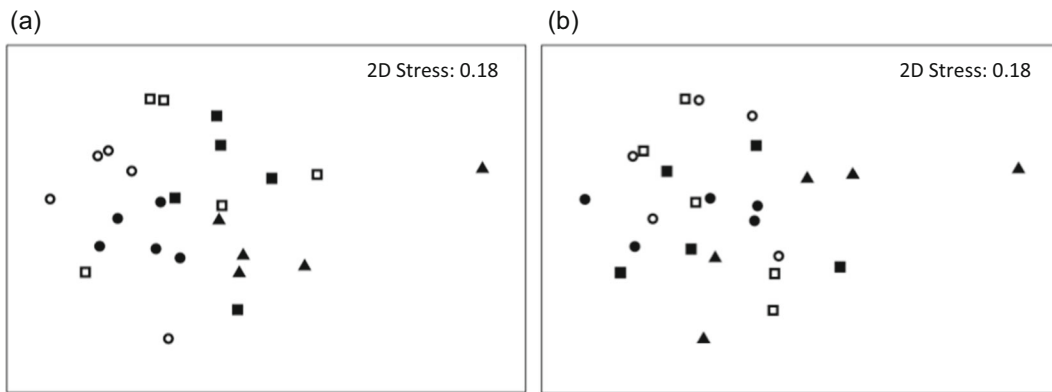


Fig. 6 Metric multi-dimensional scaling ordination of water quality characteristics between (a) the Lake Tana study tributaries (● Shini, ○ Chibirna, ■ Arno, ◻ Qimon, ▲ Guanta) and (b) five sampling trips (▲ 1, ■ 2, ◻ 3, ● 4, ○ 5), August to November 2014

were diminished at the end of the irrigation season and concluded that dewatering was a major threat to fish survivorship within irrigation systems. We observed large numbers of dead juveniles along the Arno and Shini canals at the end of the irrigation season, and anecdotal reports from nearby farmers were similar (G. Teshome, unpublished data). Entrainment of fish within downstream canal reaches and subsequent mortalities following dewatering may be a significant issue in the present study system. However, irrespective of a canal's habitat suitability and mortality losses, the best ecological outcome would still likely be the retention of fish within tributary channels. A variety of fish diversion screens have been implemented internationally to minimize fish ingress into irrigation systems (Baumgartner and Boys 2012), although none have yet been tested along Tana tributaries. Exploring these as a mechanism to reduce recruitment losses in the study region would have strong merit.

The present study is the first to directly link tributary water quality with fish assemblage and population measures in the Tana basin. Conductivity and turbidity-related variables (Secchi depth, TDS) had the strongest association with both adult assemblage structure and individual species' abundance. However, past studies [reviews by Kjelland et al. (2015) and Koehnken et al. (2020)] have tended to find negative associations with the water quality parameter(s), whereas the present study detected positive relationships. One explanation for this may be the use by Tana tributary fishes of conditions around peak flow periods for their cue to shift upstream to spawn (Anteneh et al. 2012). Higher flow rates are often

linked with increased turbidity levels (Chen and Chang 2019) although not necessarily conductivity or other solutes (Dzikowski and Jobard 2012; Heppell et al. 2017). In Malawi's Lake Chilwa basin, Jamu et al. (2003) found that stream discharge, conductivity and suspended solids levels were significant predictors of the timing of spawning migration in two *Barbus* species. Similar relationships are yet to be modelled for any Tana fishes and represent a substantial knowledge gap, although may clarify patterns observed in the present study.

Studies elsewhere have linked increased instream turbidity and suspended material levels to various anthropogenic sediment disturbances (Sutherland et al. 2002; Jamu et al. 2003; Kjelland et al. 2015; Koehnken et al. 2020) although not necessarily for conductivity (Bayram and Önsöy 2015). Agricultural practices and vegetation clearing have resulted in substantial erosion problems across the Tana region (Steenhuis et al. 2014), and high levels of downstream siltation have been documented in two of our study catchments (Ribb and Gumara: Abate et al. 2017; Zimale et al. 2018). However, fluvial sand and gravel extraction also occurs along most Tana tributaries (Mingist and Gebremedhin 2016). More broadly, such activities typically result in at least channel incision and loss or increased mobilization of gravel and sand bars, as well as exacerbated levels of siltation and parameters such as turbidity downstream (Koehnken et al. 2020).

Mingist and Gebremedhin (2016) is the only published study to have considered the potential impacts of fluvial sand and gravel mining on freshwater fish anywhere within Africa. Yet, quantifying the extent to

Table 8 SIMPER analysis of the contribution of individual parameters to differences in water quality characteristics between the Lake Tana study tributaries and sampling trips, August to November 2014. Comparisons are shown only for river or trip pairs which differed significantly at $\alpha = 0.05$ (ANOSIM, Table 8)

Parameter	Mean value	Cumulative %	Average squared distance	Parameter	Mean value	Cumulative %	Average squared distance
Shini River – Chibirna River							
	Shini	Chibirna	7.18	Guanta River – Chibirna River	Guanta	Chibirna	20.72
Temperature	-0.776	0.666	43.54	Secchi depth	-1.310	-0.440	25.48
Dissolved oxygen	0.189	-0.109	70.55	Conductivity	1.010	-1.040	49.77
				Total dissolved solids	-0.953	-1.050	72.77
Shini River – Arno River							
	Shini	Arno	7.65	Guanta River – Qimon River	Guanta	Qimon	19.24
Temperature	-0.776	0.322	28.54	Secchi depth	-0.310	0.277	24.08
pH	-0.200	0.050	47.04	pH	-0.503	0.774	42.68
Total dissolved solids	0.500	-0.570	65.47	Temperature	0.665	-0.876	58.15
Dissolved oxygen	0.189	0.548	80.37	Conductivity	1.010	-0.049	72.80
Shini River – Guanta River							
	Shini	Guanta	17.70	Trip 1 – Trip 4	Trip 1	Trip 4	19.52
Secchi depth	0.469	-1.310	30.29	Secchi depth	-0.997	0.294	23.17
Conductivity	0.475	-1.010	46.92	Dissolved oxygen	-1.260	0.440	41.73
Total dissolved solids	0.500	-0.953	62.84	Conductivity	-0.965	0.224	57.39
Temperature	-0.776	0.665	78.53	Total dissolved solids	-0.867	0.245	72.66
Chibirna River – Arno River							
	Chibirna	Arno	11.40	Trip 1 – Trip 5	Trip 1	Trip 5	19.47
Total dissolved solids	1.050	-0.570	25.72	Secchi depth	-0.997	0.562	25.89
Conductivity	1.040	-0.459	48.07	Dissolved oxygen	-1.260	0.635	48.23
Dissolved oxygen	-0.109	0.548	65.18	Conductivity	-0.965	0.291	67.33
pH	-0.121	0.050	80.79	Total dissolved solids	-0.867	0.323	86.11

Table 9 Summary of BIO-ENV results based on Spearman Rank correlations (r_s) between adult fish assemblage structure and water quality variables across the Lake Tana study tributaries and five sampling trips, August to November 2014. These are the best possible solution for each number of variables

No. of variables	Variables (r_s)
1	Cond (0.398)
2	Cond, Secchi (0.415)
3	Cond, pH, Secchi (0.430)
4	Cond, TDS, pH, Secchi (0.437)
5	DO, Cond, TDS, pH, Secchi (0.402)

which aquatic biota in Tana tributaries are being affected by sedimentation and associated reductions in water quality requires more evidence. The main season for sand mining in the Arno and Shini rivers matches the peak timing of *Labeobarbus* species spawning migrations into the study tributaries (August to October: e.g. Palstra et al. 2004; Gebremedhin et al. 2012; Anteneh et al. 2012, 2013; Teshome et al. 2015). Sedimentation and turbidity over those periods would likely have consequences for both adults (e.g. loss of spawning habitat in lithophilic spawners: Sutherland et al. 2002; Sutherland 2007) and early life-history stages (e.g. lowered egg retention and survival in smothered gravel beds; reduced visual acuity, growth and survival in larvae) in fishes of the Tana tributaries. However, discriminating

Table 10 Significant two-tailed Spearman Rank correlations (r_s) between adult fish species abundance and water quality variables across the Lake Tana study tributaries and five sampling trips, August to November 2014. Significance was accepted at $p \leq 0.10$ to reduce the likelihood of Type II errors

Variable	Fish species	r_s (p)
Conductivity	<i>Labeobarbus intermedius</i>	0.372 (0.067)
	<i>Labeobarbus nedgia</i>	0.462 (0.020)
	<i>Labeobarbus besu</i>	0.519 (0.008)
	<i>Clarias gariepinus</i>	0.374 (0.066)
	<i>Oreochromis niloticus</i>	0.502 (0.010)
Total dissolved solids	<i>Labeobarbus intermedius</i>	0.391 (0.053)
	<i>Labeobarbus nedgia</i>	0.393 (0.052)
	<i>Labeobarbus besu</i>	0.515 (0.008)
	<i>Clarias gariepinus</i>	0.363 (0.074)
	<i>Oreochromis niloticus</i>	0.506 (0.010)
Dissolved oxygen	<i>Oreochromis niloticus</i>	0.380 (0.061)
pH	<i>Labeobarbus besu</i>	-0.484 (0.014)
Secchi Depth	<i>Oreochromis niloticus</i>	0.623 (0.001)

the effects of instream materials extraction from those due to landscape erosion will be challenging, especially given the diffuse nature of the latter, and require careful, control–impact sampling designs (Underwood 1994).

Conclusions

We found Lake Tana tributaries to comprise a suite of unique fish biodiversity units. From the end of the 2014 wet season and into the dry season, variability in assemblage structure among tributaries per se was stronger than either temporal patterns or between rivers with and without irrigation dams or sand-mining. Nevertheless, the total number of species was highest in the two tributaries without either dams or sand extraction. Effective conservation measures at the lake scale will need to bear in mind that protecting assemblages in only one or more tributaries will not guarantee the conservation of all species.

We agree with previous assertions that irrigation dams disrupt upstream spawning migration in Lake Tana fishes and add evidence that the subsequent downstream movement of juveniles is also substantially impacted. Although irrigation canals off tributaries create additional aquatic habitat, we think they offer very limited ecological functionality and potentially lead to significant population losses following dewatering. We recommend implementing measures that facilitate multidirectional movement around weirs and dams and screening of irrigation intake points to minimize losses of juvenile fish into canals.

Water quality parameters such as turbidity and conductivity were highest during the peak spawning period, possibly due to a coincidence between higher-flow intervals and associated channel disturbance and the *Labeobarbus* seasonal spawning strategy that maximizes access of the fish to spawning sites and dispersal of propagules. Direct assessments of how poor water quality may be inflated through catchment erosion or sand mining, using robust sampling designs, are urgently needed to develop effective intervention strategies. Establishing a greater understanding of how irrigation infrastructure and water quality impact the early life history stages of fish within tributaries as a priority knowledge gap will help limit future recruitment failures and loss of Lake Tana fish species.

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Code availability Not applicable.

Authors' contributions GT, AG, MM and WA conceived and designed the study, which was undertaken with funding obtained by AG. GT performed the fieldwork, and GW analysed the data. GT and GW wrote the manuscript.

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Data availability All data are available from the corresponding author upon request.

Declarations

Ethics approval All sampling was undertaken in accordance with animal ethics approval from Bahir Dar University's Animal Ethics and Experimentation Committee.

Consent to participate Not applicable.

Consent for publication All authors read and approved of the manuscript prior to its submission.

Competing interests This manuscript is original work carried out by the authors. This work has not been published previously and is not under consideration for publication elsewhere. The authors declare that they have no known competing financial interests, personal relationships or conflicts of interest that could have appeared to influence the subject matter or materials reported in this paper.

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