Importance of environmental flow on feeding and distribution of juvenile *Labeobarbus* species in the Gumara River, Lake Tana Sub-basin, Ethiopia

Wondie Zelalem [a,b,*], Wassie Anteneh [c], Minwyelet Mingist [b], Mulugeta Kibret [d], Enyew Adgo [e], Jan Nyssen [f], Elie Verleyen [g], David X. Soto [h], Steven Bouillon [h], Alain De Vocht [a,i]

[a] *UHasselt, Centre for Environmental Sciences, Agoralaan, 3590 Diepenbeek, Belgium*
[b] *Department of Fisheries and Aquatic Sciences, Bahir Dar University, P.O.Box 79, Bahir Dar, Ethiopia*
[c] *Intergovernmental Authority on Development (IGAD), P.O. Box 2653, Djibouti*
[d] *Department of Biology, Bahir Dar University, P.O.Box 79, Bahir Dar, Ethiopia*
[e] *Department of Natural Resource Management, Bahir Dar University, P.O.Box 79, Bahir Dar, Ethiopia*
[f] *Department of Geography, Ghent University, Krijgslaan 281, S8, 9000 Gent, Belgium*
[g] *Department of Biology, Ghent University, Krijgslaan 281, S8, 9000 Gent, Belgium*
[h] *Department of Earth and Environmental Sciences, KU Leuven, Oude Markt 13, 3000 Leuven, Belgium*
[i] *PXL University College, Elfde-Liniestraat 24, 3500 Hasselt, Belgium*

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ABSTRACT

The tributary rivers of Lake Tana are important nursery grounds for larvae and juveniles of the migratory endemic *Labeobarbus* species, but very little is known about their functional habitat and feeding preferences. This study investigated nursery grounds, habitat shifts, and potential energy sources for juvenile *Labeobarbus* species. Electrofishing point abundance sampling for juvenile sampling and stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) were applied to trace potential energy sources. Habitat use shifting was observed among *labeobarbus* size classes from weak or no flow pool to fast-flowing riffle mesohabitats. The young-of-the-year (YOY) were mainly found in microhabitats with a weak to moderate water velocity (i.e., < 0.3 m s^{-1}), while 1$^+$ juveniles (>7 cm FL) adapted to velocities of > 0.3 m s^{-1}. Juveniles suffered from limited access to run and riffle habitats during the peak dry season (March-April). They were subsequently exposed to resource competition and predation risk which led to lower catches. Juveniles of different size classes used different food sources. C1 (<3 cm) and C3 (5.1–7 cm) size classes mainly relied on algal sources, while C2 (3 – 5 cm) and C4 (>7 cm) on zooplankton. Insect larvae were a relatively important source for larger juveniles. Maintaining appropriate flow that permits juveniles to access preferred foraging and nursery habitat in the Gumara River is crucial for the sustainable management and conservation of the *Labeobarbus* population in Lake Tana.

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Introduction

Habitat requirements in most riverine fish species are life stage-specific (Henderson and Johnston, 2010; Reichard et al., 2002). Depending on their stage of development and physiological capability, fish require habitats that enable them to survive, feed, grow, and reproduce successfully. Habitat requirement and habitat shifts are more frequent in early life stage fish, where physiological changes occur quite quickly than in adults (Schiemer et al., 1991). The higher availability of suitable habitats after the ontogeny shift results in an increased abundance of larvae and juvenile fish, which affects the adult population size (Garner, 1997). Equally, when the habitat is fragmented and difficult to access suitable or optimal habitats, juvenile survival and growth might decline, affecting population sizes and increasing regional extinction risk. Thus, identifying the most favorable conditions for young fishes, including their feeding ecology and food source, is required to conserve and sustainably manage fish population of an aquatic ecosystem.

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* Corresponding author at: UHasselt, Center for Environmental Sciences, Agoralaan, 3590 Diepenbeek, Belgium.
E-mail address: wondiehm@gmail.com (W. Zelalem).

Gumara River, one of Lake Tana's tributaries, is an important breeding ground for adult migratory *Labeobarbus* (Cyprinidae) species and provides nursery habitats for their larvae and juveniles (Anteneh, 2013). These potamodromous *Labeobarbus* species move upstream following the onset of the rainy season in June to breed (Sibbing et al., 2005). Many of these species breed in shallow water with gravel beds (de Graaf et al., 2010; Dzerzhinskii et al., 2007). The adults of some species and the newly hatched larvae and juveniles remain in the main river throughout the year (Anteneh, 2013; Shkil et al., 2017) using the available sheltering and foraging habitats. However, information on the specific habitat use and available food sources of these economically important endemic *Labeobarbus* juveniles is still largely lacking in the sub-basin.

Seasonal flooding in turbid tropical rivers affect patterns of food availability and productivity and a considerable contribution of allochthonous sources of organic carbon. (Abrantes et al., 2013; Neres-Lima et al., 2017). Gumara River receives terrestrial organic matter of different origins, quality, and quantities from its watershed. A high load of organic matter from sediment runoff (Abate et al., 2015), detrital organic matter from trees (as fallen leaves and fruits), grass, and shrubs can contribute directly or indirectly to energy sources for juveniles. Characterizing the sources that support juvenile survival and growth of the *Labeobarbus* species is key to conserving the Lake Tana *Labeobarbus* population and their management in River Gumara.

The aim of the present study was to determine the distribution of juvenile *Labeobarbus* across different mesohabitats and microhabitats within the lower reaches of the Gumara River and their roles in the life history of the fish. Specifically, it addressed three research questions: i) what is the specific nursery habitat of juvenile *Labeobarbus* in the Gumara River channel? ii) do juvenile *Labeobarbus* species show habitat shifting on a microhabitat scale? iii) what sources of potential food (directly consumed) support the YOY survival in the river?

Materials and methods

Study area

We studied the Gumara River in the Lake Tana sub-basin, northwest Ethiopia (Fig. 1) from November 2019 to April 2020. The river receives water from a catchment area of 1,376 km^2. It flows over 133 km from its source (Mount Guna) to Lake Tana, with the highest flow (236 m^3 s^{-1}) in August and the lowest (4.0 m^3 s^{-1}) in March (Abebe et al., 2020). The river system was selected because it is the major breeding location for more than ten riverine spawning *Labeobarbus* species, which are the most important commercial species in Lake Tana (Dzerzhinskii et al., 2007; Palstra et al., 2004; Shkil et al., 2017). The study was limited to the lower reach of the Gumara River (about 42 km upstream from the river mouth), between the confluence with the Dukalit stream and the Gumara mouth at Lake Tana. The mesohabitat sampling sites were identified and classified as pool, riffle, and run based on the flow gradient (Table 1, Table 2). Seventy microhabitat sub-units (points) were assigned systematically to each mesohabitat type (at about 20 m intervals between points).

The depth of the water column was measured with a meter stick and categorized as shallow (S) $\leq$ 1 m, moderate (M) = 1.1 to 2 m, deep (D) = 2.1 to 3 m, and very deep (VD) $\geq$ 3 m (Keller et al., 2019). The river water column velocity was measured with a Geopack advanced stream flow-meter (model ZMFP126-S) from surface to one meter depending on the depth in each microhabitat. The streamflow was categorized as weak (W) = 0 to 0.15 m s^{-1}, moderate (M) = 0.15 to 0.3 m s^{-1} and fast (F) $\geq$ 0.3 m s^{-1} (Donaldson et al., 2013) based on the average of the measurements

from all mesohabitat units. Substrate types were visually assessed in each microhabitat as particles < 2 mm = silt/clay/sand, 2.1–63 mm = gravel/pebble, and 63.1–256 mm = cobble (Wentworth, 2013). Substrate embeddedness was expressed as low (<25 %), medium (25–50 %), and high (>50 %) based on the presence of gravel, pebbles, and cobbles surfaces surrounded by fine sediment (Kaufmann et al., 1999). The presence or absence of vegetation cover was recorded at each site by visual inspection.

Other environmental parameters such as temperature, dissolved oxygen (DO), specific conductivity (Sp. Cond.), total dissolved solids (TDS), and pH were measured in situ using the YSI ProDSS multimeter probe. Turbidity was measured usinga digital turbid meter model AL250T-IR.

Fish specimen collection

Fish sampling was conducted by point abundance sampling using electrofishing (PASE) for a fixed time (ca. 30 s). The Bretschneider electric fishing device (model EFGI 1300) with 80 to 470 Volt output was employed in each sampling point. Given the low conductivity of river water, the electrofishing device was calibrated based on ambient conductivity to optimize sampling efficiency and minimize mortality. Sampling was conducted across alternate banks and mid-channel to cover all habitat types. It was conducted towards the upstream following a zigzag trajectory (Le Pichon et al., 2017). The sampling area for each sampling point was estimated as the circular electrical field around the 48 cm diameter anode ring (Le Pichon et al., 2017). Electro-stunning (shocking) is size-dependent according to Borgstrøm and Skaala (1993). The average area of anesthetizing and catching the fish was recorded at each point.

Sampled fish specimens were immediately netted to avoid damage by an electric field and placed into buckets filled with river water until their identification and count. The fish specimens were retained in the container to avoid the chance of recapture until the completion of assessing the nearby sampling areas. Fishes were categorized and counted to genus level and are in this article referred to as *Labeobarbus* species since it was impossible to distinguish *Labeobarbus* at the species level at a size of < 7 cm fork length (FL). *Labeobarbus* juveniles were identified from other fish species using a key developed by Anteneh (2013).

After collecting specimens at each site, the captured fish were measured for FL to the nearest 0.1 cm and assigned to different classes as < 3 cm (Class 1 = C1), 3 – 5 cm (Class 2 = *C*2), 5.1 – 7 cm (Class 3 = C3) and > 7 cm (Class 4 = C4) considering the mouth (oral) gape with 10 % of fork length and the possible particle size intake (Sibbing and Nagelkerke, 2001; Singh et al., 2015). Size classes < 7 cm FL (i.e., C1, *C*2, and C3) are considered YOY fish (Shkil and Levin, 2008).

Food sources sampling

The diet of juvenile *Labeobarbus* species, samples from small-sized juveniles (whole sample) and muscle tissue from larger individuals were collected to determine and estimate the contribution of the food (energy) sources. The samples were placed in a vial and dried at 60 °C in an oven.

Four potential food sources (i.e., algae (periphyton and phytoplankton) (Alg), detritus (Detr), insect larvae (Minv), and zooplankton (Zoo)) were collected for stable isotope analysis. Phytoplankton and zooplankton samples were collected using a 40 μm net from a depth of up to 50 cm in the water column and filtered with a 100 μm net to separate zooplankton from phytoplankton or other biofilms. A scoop net with a pore size of 500 μm was employed to collect insect larvae. Periphyton was collected from various rocks, logs, and plant surfaces and placed in the same vial. Samples were
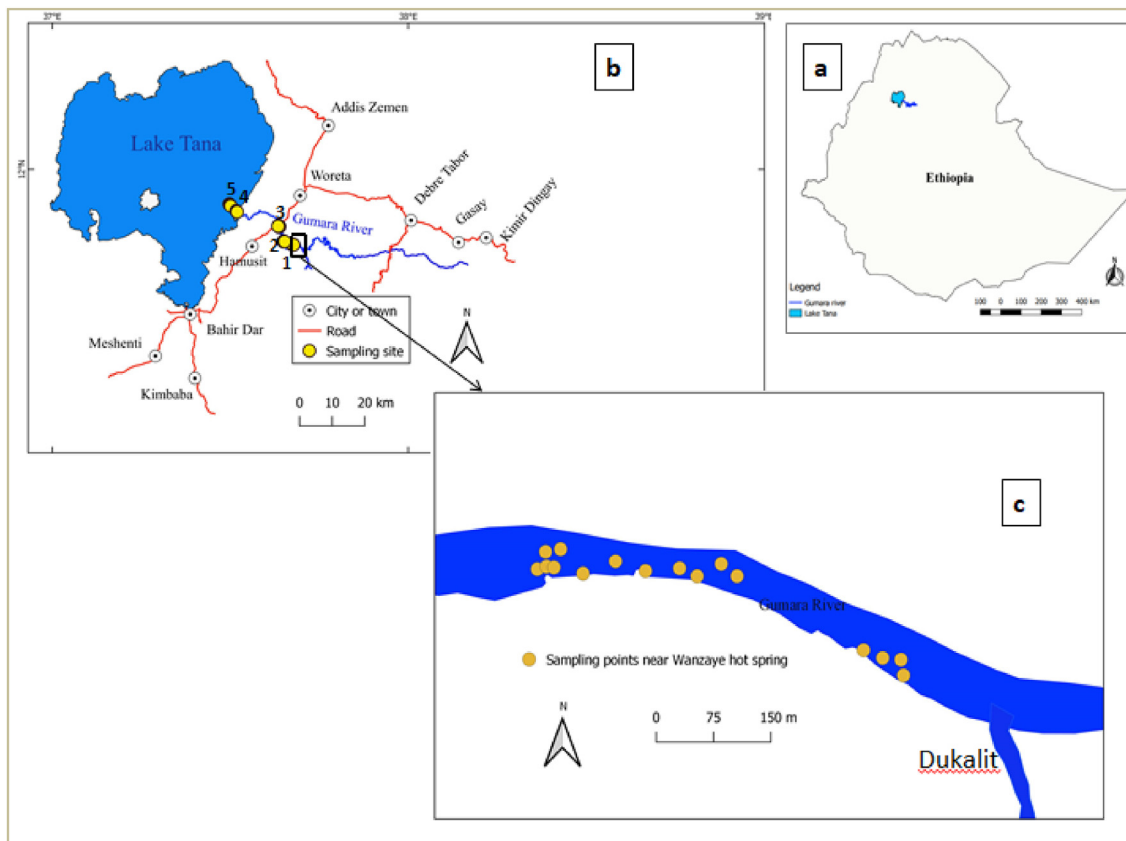
Fig. 1. Map of the study location a) Lake Tana in Ethiopia, b) Lake Tana and sampling sites on the Gumara River between November 2019 and April 2020. Site names: 1 = Near Wanzaye hot-spring (HS), 2 = Near Kizen stream (NK), 3 = Near Gumara Bridge (NB), 4 = Downstream pool 1 (DS1), 5 = Downstream pool 2 (DS2). c) Distribution of microhabitat measurements at site HS = 1.

Table 1
Characteristics of the sampling sites in the Gumara River between November 2019 and April 2020. Names of sampling sites are written in an extended form in Fig. 1. wd = Water column depth, wv = water column velocity, and available mesohabitat units are defined as Ru = run, Rf = riffle, and P = pool.

Sampling sites					
	HS	NK	NB	DS1	DS2
Number of sampling points	16	18	16	10	10
Mean wd (m) ± SE	0.53 ± 0.03	0.74 ± 0.06	0.89 ± 0.09	1.91 ± 0.14	2.37 ± 0.18
Max	2.0	4.0	7.5	5.5	5.6
Mean wv (m s^{-1}) ± SE	0.18 ± 0.03	0.15 ± 0.02	0.06 ± 0.01	0.001 ± 0.0001	0.00
Max	2.04	1.49	0.64	0.01	–
Available Habitat units	Ru, Rf, P	Ru, Rf, P	Ru, P	P	P

Table 2
Characteristics of mesohabitat units in the study reach in Gumara River between November 2019 and April 2020. % available = percent availability of each mesohabitat unit, Mwv (m/s) ± SE = mean water column velocity ± Standard error, Max = maximum value of water column velocity.

Meso-habitat	% available	Mwv (m s^{-1}) ± SE Max	Defined physical attributes	Dominant Substratum type
Pool	70.9	0.013 ± 0.003 0.33	Deep, very slow to no flow	Sand and silt
Run	15.2	0.194 ± 0.024 0.82	Relatively shallow, low gradient, and laminar flow	Gravel and pebbles
Riffle	13.9	0.342 ± 0.047 2.04	Shallowest, moderate to high gradient, and turbulent flow	Gravel, pebbles, and cobbles

later dried in an oven (DHG-9053A) for 48 to 72 h at 60 °C, and isotope ratios of carbon and nitrogen were analyzed using an elemental analyzer (Thermo EA 1110 or Thermo Flash HT/EA) coupled to an isotope ratio mass spectrometer (Thermo Delta V Advantage). Results are expressed as delta values (δ) relative to the international standard V-PDB (Vienna Pee Dee Belemnite) and atmospheric N_2 for carbon and nitrogen, respectively, using the formula (Post, 2002);

$$\delta X = [(R\ sample: R\ standard) - 1] \times 10^3.$$

where X is ^{13}C or ^{15}N, and R is the corresponding ratio $^{13}C:^{12}C$ or $^{15}N:^{14}N$.

Data were calibrated using certified (IAEA-600, i.e., caffeine) and in-house (Leucine, tuna muscle tissue) standards, with typical reproducibility better than 0.15 ‰.

Statistical analysis

The catch per unit of effort (CPUE) was calculated as the number of individuals per volume of water (ind. m^{-3}) in each sampling point to normalize the density of captured *Labeobarbus* fishes. The test probabilities for each fish size class were adjusted with the Bonferroni correction for multiple comparisons. Variation among sampling sites and mesohabitat units was computed using a Kruskal–Wallis test in SPSS 26. We employed a set of Chi-square ($\chi2$) tests for each size class to examine the relationship between fish distribution (presence/absence) and environmental variables measured as categorical variables. Furthermore, the relationships between the mean abundance of fish size classes and environmental variables were explored using canonical correspondent analysis (CCA) using CANOCO version 4.5. Hence, the CPUE and predictor parameters were measured on different scales log-transformed data was used to run the CCA. Stepwise selection of environmental predictors to explain juvenile density variation and biplot scaling was used. In the CCA, only significant predictors were plotted to demonstrate the difference in habitat preference among *Labeobarbus* juvenile size classes. Generalized Additive Model (GAM), in which the weighted average method was executed, was also applied to determine the optimum density of size classes in response to potential environmental predictors. A forward stepwise likelihood ratio technique was applied to select the best set of variables in the model. The non-linear interaction term (i.e., quadratic with Poisson distribution) was used for each variable set.

A two-way analysis of variance (ANOVA) and Tukey's HSD post hoc test on size and site as factors was used to assess differences in $\delta^{13}C$ and $\delta^{15}N$ values within the four size classes using SPSS 26. Bayesian mixing models (SIAR) in the R package by Parnell et al. (2010) were employed for stable isotope data to estimate the relative contributions of different potential nutritional sources to juvenile size classes. The trophic fractionation value and uncertainties 0.4 ± 1.3 ‰ for $\delta^{13}C$ and 3.4 ± 1.0 ‰ for $\delta^{15}N$ were used from Post (2002) *meta*-analysis. The Markov Chain Monte Carlo (MCMC) methods were run for 500,000 iterations in the SIAR model. The initial 50,000 iterations were discarded to produce simulations of plausible values of dietary proportions of sources. Food sources were assigned to taxonomic groups for analysis before running SIAR.

Results

Habitat use of juvenile Labeobarbus species

A total of 1,404 *Labeobarbus* juveniles were collected during the study period, of which 1,334 individuals were YOY fish, and only 70 (5 %) were year 1$^+$ juveniles. The CPUE of juveniles (ind.m^{-3}) varied significantly among sites (H (4) = 16.1, p < 0.01) and declined downstream along the study reach. The post hoc test results showed that site HS had the highest mean (SE) CPUE (5.2 ± 2.8 ind.m^{-3}), which significantly differed (z = 2.9, p < 0.03) from that in the downstream site DS1 (0.3 ± 0.1 ind.m^{-3}). The CPUE in NB (2.9 ± 0.8 ind.m^{-3}) significantly differed from that in DS1 (z = 3.6, p < 0.01). A temporal increment of juvenile fish density was observed in the upstream (HS) site from November to December and declined in the subsequent sampling months. Significant density variations were observed between December and March (z = -4.1, p < 0.001) and January and March (z = -3.1, p < 0.05) in the DS1. Except for site NB, which showed the highest CPUE during

January, the overall density declined in the upstream study sites from January to April (Table 3).

All size classes were present in the five sampling sites. However, their distribution varied in time and space (Table 4, Table 5). The C1 density peaked in upstream sites from November to January, coinciding with the riverine migratory adult post-breeding season and subsequently declined in the months after. The catch of all *Labeobarbus* species decreased in March and April, with the lowest catch recorded in April (Table 4). The spatial distribution of the different size classes of juvenile *Labeobarbus* species significantly varied along with mesohabitat units. The run mesohabitats with the highest mean CPUE (7.1 ± 4.0 ind. m^{-3}) varied considerably from the pool (1.4 ± 0.3 ind. m^{-3}) (H (2) = 2.6, p < 0.05). The riffle with a mean CPUE of (2.6 ± 0.7 ind. m^{-3} differed from run and pool habitats but was not statistically significant.

The different size classes of the juvenile *Labeobarbus* species also showed a preference for different microhabitats. Using the presence/absence data, *C*2 showed a significant positive association with vegetation cover (Table 6). It was dominantly found in the run habitats with a shallow depth and a moderate water column velocity. C1 was found predominantly in habitats with a weak water velocity and tended to occur in sites with a moderate water column depth. C3, on the other hand, tended to occur in pool habitats with a weak water velocity and showed a strong positive association with water depth and chlorophyll concentration (Electronic Supplementary Material (ESM) Table S1). The C4 juveniles were more prevalent in shallow (<1 m) run and riffle mesohabitats with a water current higher than 0.3 m s^{-1}. Habitats were connected during continuous river flow (typical water flow) from November to January. During this period, YOY size classes were predominantly found in microhabitats with vegetation cover and avoided the fast-flowing water (i.e., higher than 0.3 m s^{-1}). In contrast, C4 juveniles were usually discovered in association with run and riffle habitats away from vegetation covers (Table 6, Fig. 2). From March, until the onset of flooding, mainly in June, the water level was extremely low, and all YOY and C4 juveniles aggregated and dominantly shared the pool habitats.

The C1 were predominantly found in the sand/clay/silt (SS) substratum type, often associated with the pool. On the other hand, some plasticity was observed in the C2 size classes, which were predominantly present in Gravel/cobble with moderate embeddedness (GCM) to Gravel/cobble with low embeddedness (GCL) substratum types. Similarly, C3 tended to occur associated with gravel/cobble with high embeddedness (GCH) to SS substratum types. The C4, however, dominantly occurred related to the GCM substratum type (Table 6) in the typical flow conditions during the study period (i.e., November to January).

The presence of YOY fish was strongly related to plant cover ($\chi2$ (3) = 11.98, p < 0.01). They used vegetation shelter and embankments adjacent to riffles and runs with moderate to high water velocity during the typical flow period. The C2 size class, which primarily occurred in moderate water velocity, showed a strong tendency in this direction.

Relationship between juveniles' size classes and environmental variables

Water velocity, DO, and turbidity significantly explained the juvenile's distribution in the study reach as indicated in the CCA. Axis 1 (eigenvalue = 0.076) was positively correlated with the three selected predictor variables, while Axis 2 (eigenvalue = 0.024) had a strong negative relationship with water velocity and was positively correlated with DO and turbidity. C1 had a positive relationship with DO, while C4 had a positive and C1 and C3 had a negative association with turbidity and water velocity (Fig. 2). GAM revealed substantial differences between the four size classes

Table 3

The monthly juvenile catches per m^3 of water (mean ± (standard error (SE)) in Gumara River between November 2019 and April 2020. The monthly CPUE that do not share the same superscript letter within the site are significantly different, at least at the 0.05 level (Kruskal–Wallis ANOVA followed by Tukey's HSD test).

| Month | Sampling sites | | | | |
	HS	NK	NB	DS1	DS2
November	1.9 ± 0.9	6.2 ± 4.2	2.3 ± 1.2	0.1 ± 0.1[a]	0.1 ± 0.04[a]
December	11.3 ± 10.1	2.2 ± 0.8	1.1 ± 0.2	0.1 ± 0.3[a]	0.3 ± 0.2[a]
January	4.3 ± 2.2	1.3 ± 0.8	6.8 ± 2.4	0.2 ± 0.1	0.4 ± 0.1[a]
March	2.8 ± 0.9	1.0 ± 0.3	1.2 ± 0.3	0.5 ± 0.3[b]	1.0 ± 0.2[b]
April	1.5 ± 0.3	0.8 ± 0.3	0.5 ± 0.2	0.4 ± 0.2	0.3 ± 0.1

Table 4

The monthly CPUE (mean ± SE) of juvenile size classes between November 2019 and April 2020 in the Gumara River.

| | Size classes | | | |
Month	C1	C2	C3	C4
November	2.4 ± 1.3	8.4 ± 4.6	0.67 ± 0.1	3.0 ± 1.3
December	2.0 ± 1.2	13.9 ± 10.3	1.1 ± 0.4	1.8 ± 0.8
January	5.5 ± 4.2	9.4 ± 2.7	2.0 ± 0.4	0.8 ± 0.1
March	1.6 ± 0.9	2.1 ± 0.5	1.8 ± 0.4	0.6 ± 0.3
April	0.2 ± 0.1	2.1 ± 0.3	1.4 ± 0.3	0.4 ± 0.2

Table 5

The CPUE (mean ± SE) of juvenile *Labeobarbus* size classes at the study sites and mesohabitat subsections in the Gumara River between November 2019 and April 2020. The CPUE of juveniles with a different superscript letter within each site and mesohabitat are significantly different, at least at the 0.05 level (Kruskal–Wallis ANOVA followed by Tukey's HSD test).

| Size classes | Sampling site | | | | | Mesohabitat | | |
	HS	NK	NB	DSP1	DSP2	Riffle	Run	Pool
C1	5.0 ± 1.5	3.9 ± 1.7	8.5 ± 7.7	0.5 ± 0.1	0.5 ± 0.2	1.8 ± 0.6	2.0 ± 0.4	3.9 ± 1.7[a]
C2	20.2 ± 12.0[a]	6.2 ± 2.3	5.8 ± 1.7[a]	0.6 ± 0.1	0.9 ± 0.2	4.8 ± 2.7	24.5 ± 14.5	3.6 ± 0.8[a]
C3	2.4 ± 0.5	1.4 ± 0.4	2.1 ± 0.4	0.7 ± 0.3	1.0 ± 0.2	2.2 ± 1.0	1.5 ± 0.4	2.3 ± 0.2
C4	2.0 ± 0.6[b]	1.5 ± 0.6	0.5 ± 0.1[b]	0.2 ± 0.1	0.03 ± 0.1	2.9 ± 1.4	2.2 ± 0.9	0.7 ± 0.1[b]

Table 6

Distribution of the four classes of juvenile *Labeobarbus* species associations to the microhabitat predictors in the Gumara River between November 2019 and April 2020. Substratum type (ST) represents the dominantly used type by each size class; SS = Sand/clay/silt, GCM = Gravel/cobble with moderate embeddedness. χ^2 = Chi-square; p = significant levels. In the vegetation cover (VC) column, the abbreviation P = presence and A = absent of vegetation cover as a shrub, grass, and root mass. In water velocity (WV); W = weak, M = moderate, F = fast. In the water column depth (WD); M = moderate, S = shallow.

Size class	ST	χ^2	p	VC	χ^2	p	WV	χ^2	p	WD	χ^2	p
C1	SS	5.17	0.160	P	1.48	0.223	W	0.56	0.757	M	5.59	0.133
C2	GCM	4.97	0.174	P	17.47	0.000	M	1.23	0.539	S	8.08	0.044
C3	SS	1.57	0.665	P	3.13	0.077	W	2.40	0.301	M	4.17	0.224
C4	GCM	30.29	0.000	A	5.25	0.022	F	13.9	0.001	S	9.64	0.022

related to ecological factors. The *C2* showed the highest density at intermediate water column velocity. The C1 fish predominantly occur in higher DO than the other three classes of fish. Similarly, C4 occurred in habitats with higher turbidity and thrived in moderately to high DO concentrations and higher water velocity (Fig. 3).

Isotopic composition of consumers

The mean value of δ^{13}C and δ^{15}N obtained from the consumers (juveniles of *Labeobarbus* species) collected from the study sites at the Gumara River are summarized in Table 7. The two-way ANOVA showed that the mean δ^{13}C values differed significantly among size classes ($F_{3, 68}$ = 31.9, P < 0.001) and sites ($F_{3, 68}$ = 18.16, p < 0.001). Similarly, the consumer × site interaction term also revealed a significant effect ($F_{9, 68}$ = 2.30, p < 0.05) on the consumer's δ^{13}C values. The δ^{13}C value ranged between −25.0 ‰ for small individuals (C1) to −20.3 ‰ for the larger juveniles (C4) (Fig. 4). The δ^{13}C of C4 (mean value of −21.7 ± 0.6 ‰) differed significantly from C1 (−23.5 ± 0.9 ‰), C2 (−23.1 ± 1.0 ‰, p < 0.001) and C3 (−22.3 ± 0.9 ‰, p < 0.05). Similarly, δ^{13}C values of C3 significantly differed

from that of C1 and C2 (P < 0.001) (Fig. 4). However, C1 and C2 did not differ significantly for δ^{13}C.

Similarly, for δ^{15}N, the analysis revealed significant differences between consumer's size classes, sites, and consumer × site interaction (P < 0.001). It ranged from 8.8 ‰ for C1 to 11.6 ‰ for C4. The C1 with the lowest mean value of δ^{15}N (10.0 ± 0.7 ‰) varied significantly from C2 (10.9 ± 0.6 ‰), C3 (10.8 ± 0.6 ‰), and C4 (11.1 ± 0.3 ‰) (p < 0.001) (Fig. 4). However, δ^{15}N of C2, C3, and C4 did not differ significantly but varied considerably among sites.

Isotopic composition of food sources

The values of the food sources ranged from −28.9 to −16.7 ‰ for δ^{13}C and from 1.5 to 10.0 ‰ for δ^{15}N. The mean value of both δ^{13}C and δ^{15}N varied significantly between taxa (P < 0.01). For δ^{13}C, insect larvae with the highest mean (-21.7 ± 3.4 ‰) differed substantially from detritus (-25.0 ± 1.2 ‰). Similarly, for δ^{15}N, the highest (8.4 ± 1.1 ‰) and lowest (2.1 ± 0.4 ‰) mean values were recorded for insect larvae and detritus, respectively. Except for algae and zooplankton, the analysis of variance revealed a significant difference among food sources when the data from all sites
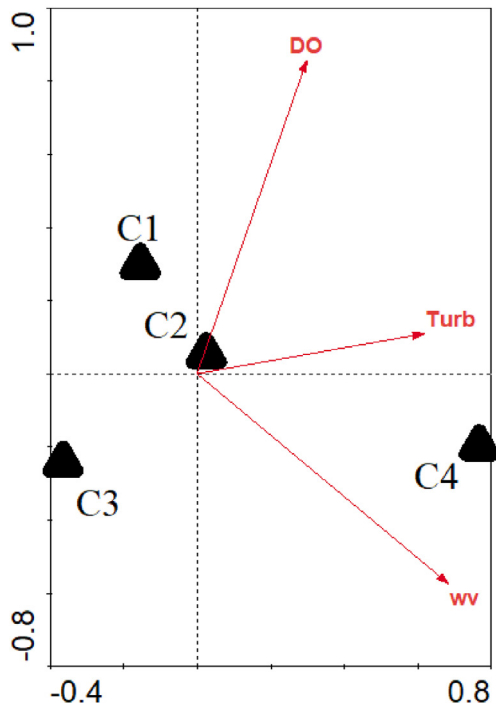
Fig. 2. A Canonical correspondence bi-plot ordination diagram depicts the relationship between YOY (C1, C2, and C3) and 1 $^+$ juvenile (C4) *Labeobarbus* species and selected environmental predictors in the study reach in the Gumara River between November 2019 and April 2020. Environmental predictors represented DO = dissolved oxygen, wv = water column velocity, Turb = turbidity.

were pooled (Fig. 5). However, there was no significant spatial variation in δ^{15}N among dietary sources (Table 8).

Contribution of food sources to the diet of Labeobarbus size classes

The SIAR model outcomes revealed the mixed use of all food sources in the study site (Fig. 6, Fig. 7). In the mixed space (Fig. 7), juvenile size classes fell within the isotope signature values of food sources in the biplot, providing confidence that we sampled the potential organic matter sources to juvenile *Labeobarbus* species in the study reach. The isotopic signatures of C2 to C4 size classes were close to algae, zooplankton, and insect larvae, whereas C1 was bounded in the mixing polygon that included detritus.

The proportion of food sources ingested varied for the different size classes based on the pooled data for each site. For C1 and C3, algae were the most dominant food source (~39.0 % and ~36.8 %, respectively), and for C2 and C4, it was zooplankton (~42.3 % and ~ 35.0 %, respectively). By contrast, insect larvae account for ~ 30.4 % and ~ 32.2 % of the diet of C1 and C4 individuals, while algae (~28.1 %) and zooplankton (~31.5 %) for C2 and C3, respectively. Size classes of juvenile *Labeobarbus* species showed spatial variation in the ingested food sources. Moreover, the contribution of insect larvae increased with increasing consumers' size in the upstream sites HS and NK. Similarly, algal sources increased with increasing consumer size in the NB and DSP sites. However, exploitation of detritus declines with increasing size (Fig. 6).

Discussion

Habitat use of juvenile Labeobarbus species

Most of the riverine spawning *Labeobarbus* species use upstream areas with gravel beds and shallow riffles as breeding

sites (Dzerzhinskii et al., 2007). The presence of nearby breeding grounds and the availability of heterogeneous alternative breeding and nursery habitats such as run, riffle, and pool can explain the higher juvenile density at those sites in this study. This result also agrees with observations from elsewhere that heterogeneous habitats support abundant and diverse communities (Meulenbroek et al., 2018; Stoffers et al., 2022; Zeni and Casatti, 2014). If fish can access a diverse mesohabitat with different microhabitats, they will benefit from better access to a broader range of food resources and reproduction sites (Boavida et al., 2011; Magalhães et al., 2002). Connectivity between, and access to, several habitat types during different hydroperiods is also needed to support diverse fish assemblages (Reinhold et al., 2016). This connectivity, however, was lost in the Gumara River during the low-flow dry season because most run and riffle habitats vanished.

Juvenile *Labeobarbus* species primarily preferred moving water during high flow conditions with complete connectivity among microhabitats. This higher density in the run and riffle was in contrast to that of Anteneh (2013), who found the highest density in the pool. The maximum catch of the smallest size class was obtained at sites connected with the pool's margin and with weak flowing riffles, which points to the preference of C1 *Labeobarbus* species for higher DO over fast water current velocity (Fig. 2). According to Anteneh (2013) larvae of various *Labeobarbus* species reside in the interstitial spaces in shallow riffle habitats with pebble and cobble where DO concentrations are relatively high. When larvae mature into free-moving juveniles, they prefer shallow, slow-moving, or no-flow environments, as observed for the C1 in this study. Habitat shifting into the moderately flowing run and riffle habitats by C2 could be linked to changes in the feeding and swimming ability as seen in many other cyprinid species (Henderson and Johnston, 2010; Reichard et al., 2002). *Labeobarbus* juveniles, mainly C2 and C4, preferred features like sloping embankments in the riffle-run confluence commonly found near moderate to fast-moving water. Sloping embankment keeps the fish from being washed out by high-flow in runs and riffles, allowing them to take advantage of feeding on drifting or floating aquatic macroinvertebrates due to turbulence. Hellmair et al. (2018) also found that juveniles living near fast currents benefit from refugial structures, reducing their energy consumption and improving feeding efficiency. In addition, such shelters offer better protection against adult piscivorous and avian predators (Keller et al., 2019).

Fish at different developmental stages may withstand varying DO, turbidity, and water current (Gaudin, 2001). They can use various behavioral and physiological means to adapt to changing environments. For example, decreasing activity, accelerating gill ventilation rates, and increasing blood hemoglobin O_2 affinity help to cope with hypoxic environments (Li et al., 2018). The higher tendency of smaller size juveniles, C1 towards higher DO concentrations (Fig. 3), and the coping of C4 to relatively lower DO concentrations (Fig. 2, Fig. 3) may be explained by physiological-based oxygen demand as juvenile fish DO consumption decreases with body-size increases (Segovia et al., 2012).

Based on this study and previous research, the microhabitat use of juvenile *Labeobarbus* species can be summarized as follows. First, fertilized eggs are attached to gravel substrate (Dzerzhinskii et al., 2007). Then, the growing larvae move to cobble and pebble structures in shallow riffles (Anteneh, 2013). The smallest class of fish with poor swimming ability (<3 cm FL in this study), when they reach the free-swimming stage, tend to live in shallow microhabitats with little to no water currents (Fig. 2). Juveniles longer than 3 cm FL tend to be adapted to flowing water with moderate water velocity as they morphologically fit to withstand water current up to < 0.3 m s^{-1}. When the fish reach a length higher than 7 cm FL (i.e., 1$^+$ year), they tend to move to moderate to fast-flowing waters with a current up to a mean value of 0.54 m s^{-1}.
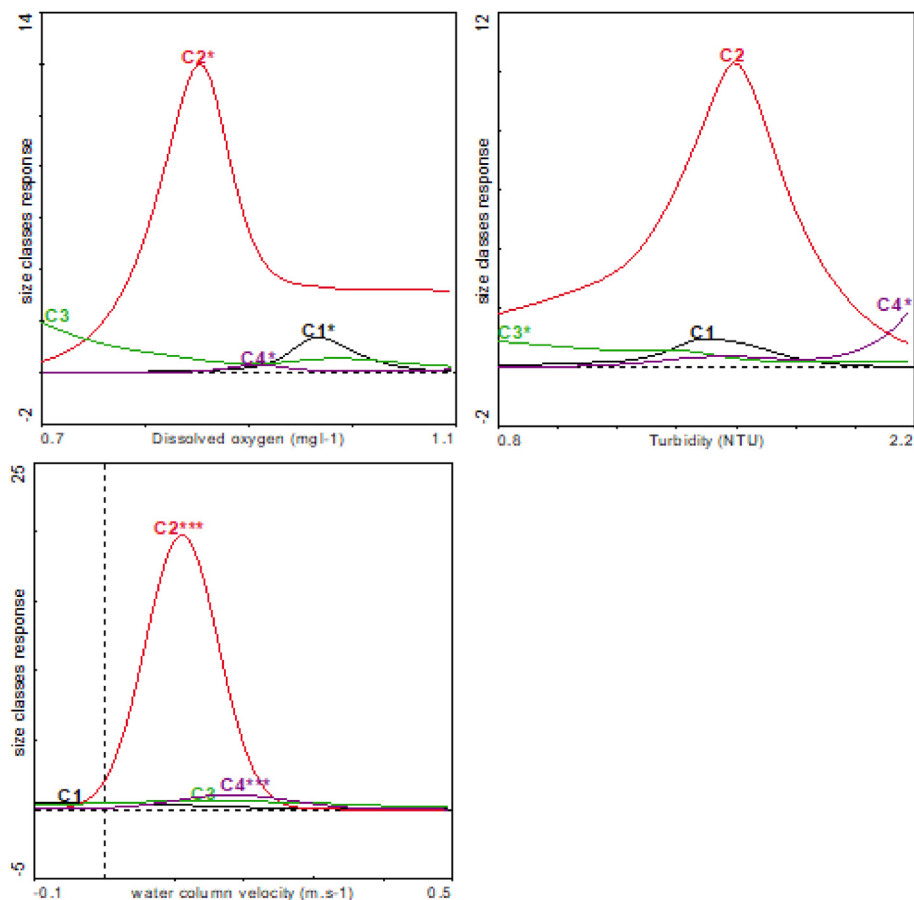
Fig. 3. Response curves of *Labeobarbus* juvenile size classes to specific environmental predictors drawn from GAM (log$_{10}$-transformed data) in the Gumara River between November 2019 and April 2020. Size classes' responses were calculated using CCA scores and selected using AIC criteria for each predictor. Significance for individual size classes is marked as: ***= $p < 0.0001$; **= $p < 0.01$ and *= $p < 0.05$.

Table 7
The mean SD of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values of *Labeobarbus* juvenile size classes in each site in Gumara River between November 2019 and April 2020. The size classes that do not share the same superscript letter within a column are significantly different for the variable in question, at least at the 0.05 level (ANOVA followed by Tukey's HSD test). Because of the similarity of sources, DS1 and DS2 sites are pooled and taken as site DSP.

Consumer	Samples size	Sampling sites HS	NK	NB	DSP
Carbon isotope ratios ($\delta^{13}C$)					
C1	21	−23.0 (0.9)[a]	−24.0 (0.6)[a]	−22.8 (0.5)[a]	−23.9 (0.5)[a]
C2	23	−22.2 (0.93)[a]	−24.2 (0.1)[a]	−22.5 (0.7)[a]	−23.4 (0.8)[a]
C3	20	−21.2 (0.5)[b]	−22.8 (0.7)[b]	−22.2 (0.2)[a]	−23.1 (0.6)[a]
C4	20	−21.3 (0.6)[b]	−22.2 (0.4)[b]	−21.8 (0.6)[a]	−21.3 (0.7)[b]
Nitrogen isotope ratios ($\delta^{15}N$)					
C1	21	9.7 (0.4)[a]	9.9 (0.4)[a]	9.3 (0.3)[a]	11.0 (0.1)[a]
C2	23	10.8 (0.4)[b]	11.0 (0.2)[b]	10.6 (0.3)[b]	11.2 (0.3)[a]
C3	20	11.2 (0.2)[b]	11.0 (0.3)[b]	10.2 (0.1)[b]	11.0 (0.1)[a]
C4	20	11.1 (0.4)[b]	11.3 (0.1)[b]	10.8 (0.4)[b]	11.0 (0.5)[a]

Following flow reduction during the dry season, most riffle habitats disappeared, and fish aggregated with deeper water in the remaining pool habitats (Kennard et al., 2007). The relatively high number of juveniles in the downstream pool habitats during the dry season suggests that juveniles migrate to pool habitats when there is limited access to preferred run and riffle habitats. However, the conditions in these refugial pools are not ideal for the *Labeobarbus* juveniles. In addition, we observed that these pools were inhabited by many other species, which were even more dominant than the juveniles, such as *Enteromius humilis, E. pleurogramma, Oreochromis niloticus,* and the predator *Clarias gariepinus*. Co-occurring juveniles with other species may expose them to stressful situations due to competition for resources and predation. Larger fish might have a higher competitive advantage over smaller ones for the available resources (Kerry and Bellwood, 2016). In addition, low amounts of DO due to high levels of humic substances and decomposing organic matter during the low river flow season (Dewey, 1984) may negatively impact the number and diversity of young fish. The lower density of juvenile *Labeobarbus* during the dry season could be due to this competition for resources, limited access to favored microhabitats due to the water-level decline, and low DO concentrations. Significantly, excessive water consumption from the river for unregulated small-scale irrigation farming worsens the availability of habitats
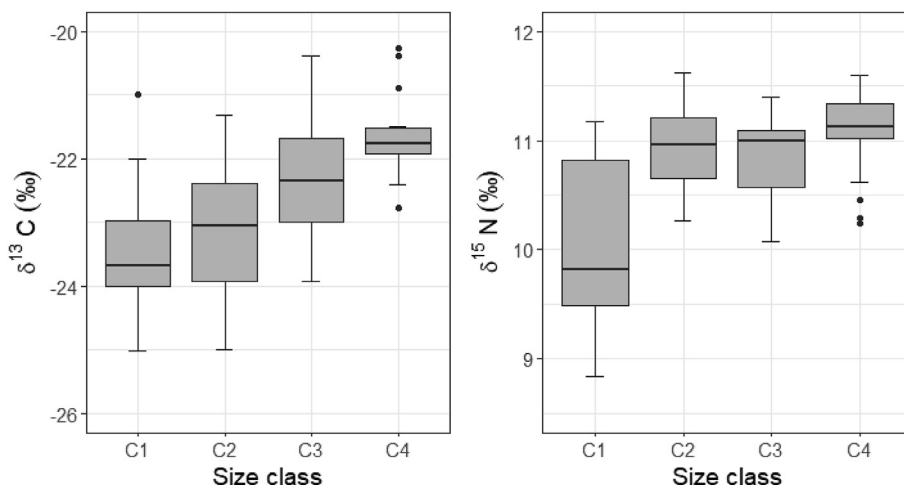
Fig. 4. Box plot for the δ^{13}C and δ^{15}N for the four size classes of *Labeobarbus* juveniles from site pooled data in the Gumara River between November 2019 and April 2020. Each box represents the first quartile, third quartile, and median (bold black line). Upper and lower whiskers represent 95 % confidence intervals, and open circles represent outliers.
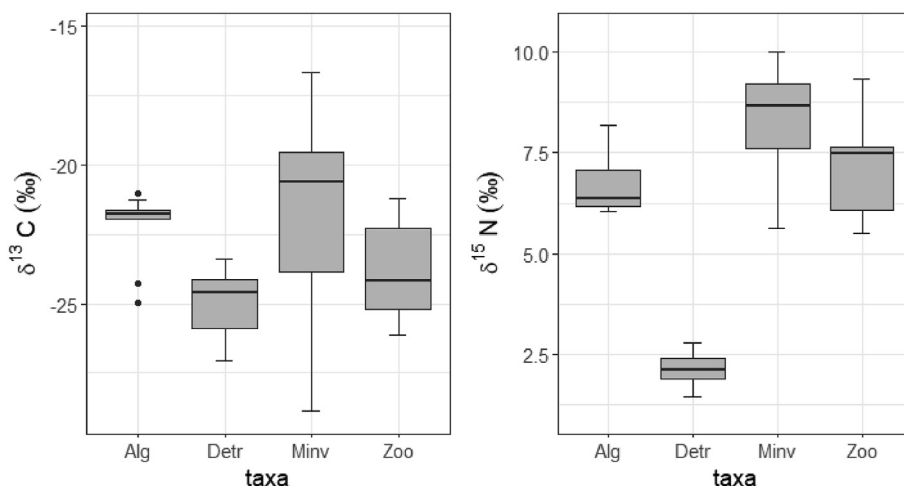

Fig. 5. Box plot showing the stable isotope signature for carbon (δ^{13}C) and nitrogen (δ^{15}N) for food sources to *Labeobarbus* juvenile size classes from pooled taxon data in the Gumara River between November 2019 and April 2020.

Table 8
The mean (SD) values of δ^{13}C (‰) and δ^{15}N (‰) of collected potential food sources (taxa) from the study sites in the Gumara River between November 2019 and April 2020. The taxa that do not share at least one superscript letter within a column are significantly different for the variable in question at least at the 0.05 level (ANOVA followed by Tukey's HSD test).

Food source	Sample size	Sampling Sites			
		HS	NK	NB	DSP
Carbon isotope ratios (δ^{13}C)					
Algae	13	−23.5 (2.0)[a]	−22.5 (2.1)	−21.8 (0.1)[a]	−21.8 (0.2)
Detritus	12	−26.0 (0.1)[ab]	−26.9 (0.2)	−24.3 (0.2)[b]	−24.2 (0.7)
Insect larvae	26	−20.1 (1.0)[c]	−22.3 (3.9)	−23.1 (0.5)[c]	−21.8 (4.3)
Zooplankton	10	−21.4 (0.3)[ac]	−26.0 (0.2)	−22.3 (0.2)[ac]	−24.6 (0.6)
Nitrogen isotope ratios (δ^{15}N)					
Algae	13	6.9 (0.8)[a]	6.9 (0.7)[a]	7.0 (1.1)[a]	6.3 (0.2)[a]
Detritus	12	2.4 (0.1)[b]	2.3 (0.1)[b]	1.9 (0.02)[b]	2.1 (0.5)[b]
Insect larvae	26	8.5 (1.2)[a]	8.8 (0.9)[c]	7.8 (0.4)[a]	7.9 (1.5)[a]
Zooplankton	10	6.5 (1.4)[a]	7.8 (0.2)[ac]	6.0 (0.6)[a]	7.6 (1.4)[a]

and deters assessing the preferred habitats. Farming and growing seasonal crops near and even within the riverbanks in some portions of the river channel exacerbates this habitat loss. Moreover,

sand mining, sedimentation, and bank erosion were other observed problems that affect the availability of nursery habitats for juvenile *Labeobarbus* species in the river.
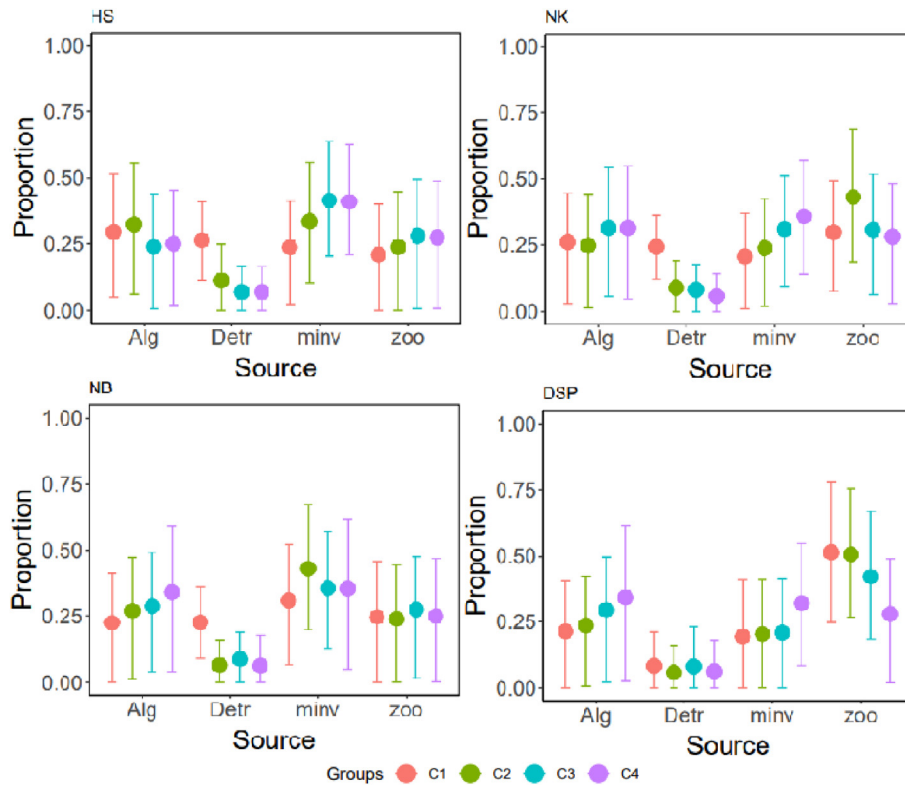
Fig. 6. The relative contribution of the various food sources in the mean diet of *Labeobarbus* juvenile size classes (C1, C2, C3 and C4) in the four sites (HS, NK, NB, and DSP) in the Gumara River between November 2019 and April 2020. The error bar represents the 95% credibility intervals, and the circular points on each error bar indicate the mean value of each source.
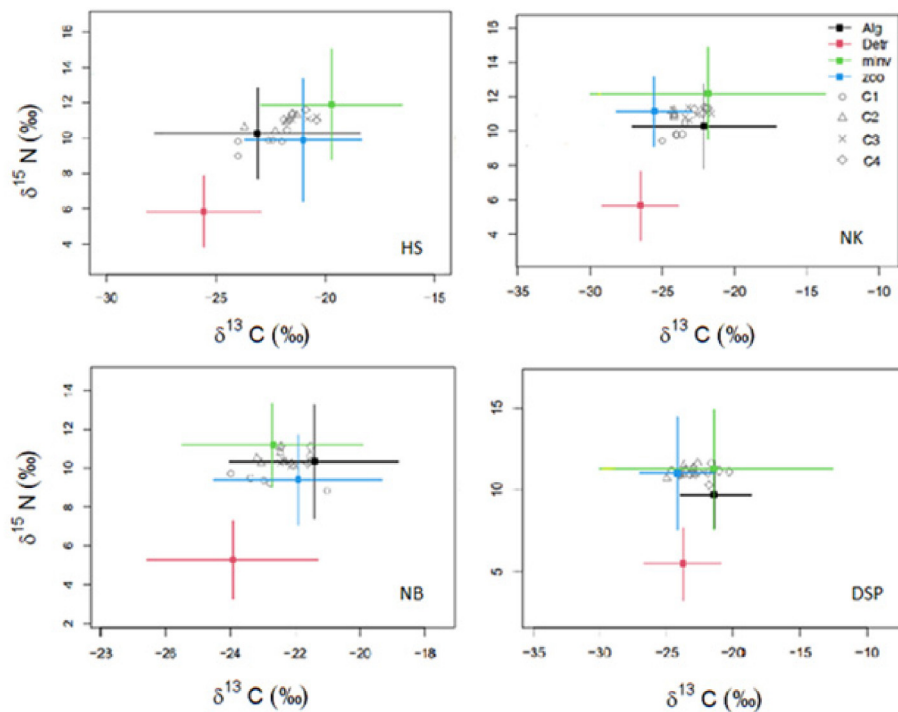

Fig. 7. Stable isotope bi-plot for consumers; *Labeobarbus* juvenile size classes (C1, C2, C3, and C4); potential sources in the HS, NK, NB and DSP sites in the Gumara River between November 2019 and April 2020. Error bars indicate combined source and discrimination uncertainty ± 1 SD.

Food source contribution

Isotopic signature biplots describe consumers' potential food sources with proximity to the source, indicating the most significant contribution of a source to the diet (Fig. 7). High confidence intervals for some sources in their contributions demonstrate overlap in consumer resource utilization (Phillips and Gregg, 2001). However, despite the overlaps in some sources, the overall differences in δ^{13}C and δ^{15}N showed the different size classes of *Labeobarbus* juveniles utilizing various food sources along ontogeny. The model results showed that young *Labeobarbus* species consume a mixture of detritus, plankton, and insect larvae, suggesting they are omnivores. These size-related dietary shifts in juveniles are most likely influenced by food availability in their preferred environments and morphological and physiological changes in the fish. For example, the smallest fish, C1, rely on smaller and immobile food sources such as algae and detritus, but the diet switches to larger insect larvae as they grow from C2 to C4. Similarly, the C3 size classes consumed more algae, demonstrating a strong link between food availability and juvenile food consumption.

Nutritional shifts have been observed in many fish species during their development (Andersen et al., 2005; Gning et al., 2008; Park et al., 2018). These diet shifts depend on competitive interactions among developmental stages and food availability (Andersen et al., 2005). However, although abundant food allows for selection and specialization, it forces animals to rely on various food sources to meet their nutritional needs when food resources are scarce (Pavlov and Kasumyan, 2002). The feeding habits of smaller classes of YOY, which primarily feed on algal and detrital matter, and the consumption of algae by C3 in this study revealed that prey availability and size are essential factors in the food selection of *Labeobarbus* juveniles.

Feeding is also highly correlated with swimming ability and speed (Sánchez-Hernández et al., 2019) because larger fish with well-developed pectoral fins would have a more stable, accurate, and active prey capturing efficiency than smaller individuals (Higham, 2007; Leavy and Bonner, 2009). The C2 and C4 classes, frequently associated with run and riffle habitats, may have primarily access to insect larvae that hide under gravel and boulders. They could mainly target aquatic insects drifting in the river during high water turbulence.

Detritus has lower energy and protein concentrations than invertebrate prey and is usually considered a supplemental food source for most adult fish (Bowen et al., 1995). However, despite its lower nutritional quality, detritus was used by the Lake Tana adult *Labeobarbus* fish species, especially the non-piscivorous taxa (de Graaf et al., 2008; Sibbing and Nagelkerke, 2001). Similarly, we discovered that also the smallest juveniles feed on detritus, possibly because of its smaller particle size and the easy accessibility of this food source.

In many studies, fish species appear restricted to particular food sources at the younger stage and shift their feeding behavior to using multiple carbon sources as they grow (Davis et al., 2012; Gning et al., 2008; Nunn et al., 2007). Similarly, in this study, the smallest juveniles feed more on algae and detritus, but they also consume zooplankton and insect larvae at different proportions at each site. In general, juveniles' usage of various food sources can augment their energy needs as they grow in size and adjust to shifting habitat conditions, as well as represent an adaptive reaction to periodic variations in food availability.

Finally, despite the difficulty in classification to species level, the morphological and behavioral resemblance among juvenile *Labeobarbus* species suggests similar feeding habits. However, based on increasing mean values of δ^{15}N, juveniles shift towards bigger-sized and more ^{15}N-enriched prey to satisfy their energy demand following the ontogenic shift.

Conclusions

Water velocity, DO, and turbidity were the most important variables influencing the presence of different juvenile *Labeobarbus* size classes. Juveniles adapted to run and riffle environments with slow, moderate, to fast flow velocity as they grew in size. They also had an increased tolerance to lower DO concentrations and higher turbidity. Despite their abundance being negatively related to depth, YOY preferred vegetation and undercut root shelters over larger juveniles. However, during the low-flow dry season, juveniles were primarily restricted to pool habitats, mostly located away from those shelters.

At different stages of development, *Labeobarbus* juveniles consumed different proportions of available food sources. They feed on detritus to insect larvae as they grow in size, but algae and zooplankton are the primary sources consumed by juveniles. Gumara River had a significant problem with juveniles' restricted access to favored habitats, including runs and riffles and the associated food sources during the peak dry season. Therefore, to promote sustained juvenile production and conservation of the *Labeobarbus* population in Lake Tana, it is necessary to pay particular attention to maintaining a minimal level of river flow and habitat connectivity throughout the dry season.

Limitations and prospects for further research

This habitat use study was carried out in daylight sampling, which limits our understanding of the complete behavioral patterns of juveniles' habitat use. Moreover, the food sources sampled were limited to some potential sources directly consumed by juveniles. Still, there could be other possible energy sources, including dissolved or particulate organic and inorganic carbon sources. Future research has to address the circadian habitat use of juveniles, including habitat suitability modeling. For the energy demand of juveniles, other possible sources that support juvenile growth in the river system are suggested to be assessed.

Ethics statement

The study was conducted after getting permission from the Ethical Committee of Bahir Dar University, College of Agriculture and Environmental Sciences (Reference # 1/102/1.3.4). All methods were performed following the relevant international and institutional guidelines and regulations.

CRediT authorship contribution statement

Wondie Zelalem: Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Validation, Writing – original draft, Writing – review & editing. **Wassie Anteneh:** Conceptualization, Data curation, Funding acquisition, Investigation, Validation, Writing - review & editing. **Minwyelet Mingist:** Conceptualization, Data curation, Investigation, Project administration, Supervision, Validation, Writing - review & editing. **Mulugeta Kibret:** Investigation, Project administration, Validation, Funding acquisition, Writing - review & editing. **Enyew Adgo:** Investigation, Project administration, Validation, Funding acquisition, Writing - review & editing. **Jan Nyssen:** Investigation, Validation, Funding acquisition, Project administration. **Elie Ver-**

leyen: Investigation, Project administration, Validation, Funding acquisition, Writing - review & editing. **David Soto:** Data curation, Formal analysis, Investigation, Validation. **Steven Bouillon:** Conceptualization, Data curation, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Validation, Writing - review & editing. **Alain De Vocht:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2022.08.021.

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