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ORIGINAL ARTICLE

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Effect of water level and water quality on small-sized and juvenile fish assemblages in the littoral zones of the Zambezi/Chobe floodplain

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Abstract

The effect of flooding phase and water quality on the littoral fish species of the Zambezi/Chobe floodplain was assessed between March 2017 and February 2018. Using the similarity percentage analyses (SIMPER), a 61.9% dissimilarity was detected in fish assemblages among the four flooding phases of the Zambezi/Chobe floodplain (rising, peak, recession and low flooding phase). Cichlids (63.1%) were the most dominant taxa during the peak flooding phase while cyprinids were dominant during the rising (40.7%), recession (45.3%) and low flooding phases (40.9%), respectively. Juveniles of the two commercially important species, ***Oreochromis andersonii*** and ***Coptodon rendalli*,** were among the four abundant species across the four flooding phases of the Zambezi/Chobe floodplain. Higher densities of these two species were in synchrony with the peak flooding phase, characterised by high levels of dissolved oxygen (5.7 ± 1.0 mg/L), neutral pH (7.9) and moderate water temperature (27.6 ± 1.1°C). During the flood recession phase, a severe decline in juvenile of the commercially important species (***O. andersonii*** and ***C. rendalli***) coincided with fish migration off the littoral zone into the main river at a mean size between 70 and 80 mm SL. Generally, the observed variations in the fish species composition during the different stages of flooding might reflect the influence of water quality and water volume to sustain large fish assemblages on the littoral zone of the Zambezi/Chobe floodplain. Any change in the natural flow and reduction in water volume of the Zambezi/Chobe floodplain might negatively affect the recruitment of juvenile fish into adult populations.

KEYWORDS

catch per unit effort, juvenile fishes, seine net, Zambezi/Chobe floodplain

Résumé

L'effet de la phase de crue et de la qualité de l'eau sur les espèces de poissons du littoral de la plaine inondable du Zambèze et de la Chobe a été évalué entre mars 2017 et février 2018. À l'aide d'analyses de taux de similarité (SIMPER), nous avons détecté une dissemblance de 61.9% au sein des peuplements de poissons au cours des quatre phases de crue de la plaine inondable du Zambèze et de la Chobe (phase de montée, maximale, de récession et de faible crue). Les cichlidés (63.1%) étaient les taxons les plus dominants pendant la phase d'inondation maximale, tandis que les cyprinidés dominaient respectivement pendant les phases de montée (40.7%), de récession (45.3%) et de faible crue (40.9%). Alevins des deux espèces d'intérêt commercial: Les espèces *Oreochromis andersonii* et *Coptodon rendalli* faisaient partie des quatre espèces abondantes au cours des quatre phases de crue de la plaine inondable du Zambèze et de la Chobe. Des densités plus élevées de ces deux espèces étaient synchronisées avec la phase de crue maximale, caractérisée par des niveaux élevés d'oxygène dissous (5.7 ± 1.0 mg/l), un pH neutre (7.9) et une température de l'eau modérée (27.6 ± 1.1°C). Pendant la phase de récession des crues, un déclin considérable de la quantité d'alevins des espèces d'intérêt commercial (*O. andersonii* et *C. rendalli*) a coïncidé avec la migration des poissons de la zone littorale vers la principale, à une taille moyenne de 70–80 mm (longueur standard). D'une manière générale, les variations observées dans la composition des espèces de poissons au cours des différentes étapes de la crue pourraient refléter l'influence de la qualité et du volume de l'eau pour maintenir d'importants peuplements de poissons sur la zone littorale de la plaine inondable et dans les terres du Zambèze et de la Chobe. Tout changement dans le débit naturel et toute réduction du volume d'eau de la plaine inondable du Zambèze et de la Chobe pourrait avoir un effet négatif sur l'intégration des alevins au sein des populations adultes.

1 | INTRODUCTION

The littoral zone is a land–water ecotone along the main river channel margins and extending onto the floodplain during high waters. The significance of the littoral zone to aquatic organisms has been documented for many aquatic systems (Junk et al., 1989; Vono & Barbosa, 2001). During the dry season, there is an accumulation of nutrients on the floodplain in the form of domesticated and wild animal dung as well as macrophytes. Periodic flooding integrates the stream with its floodplain, flushing organic material into the stream while depositing silt and minerals on the floodplain, creating ephemeral ponds. This stimulates primary production, and support aquatic fauna (Junk et al., 1989). When the Zambezi River breaches its banks during the annual flood pulse, fish move onto the adjacent highly nutrient rich floodplain habitats characterised by good water quality suitable for both spawning and feeding. As the water level gradually recedes, many fish move back to the main river stream, but juveniles, in particular can remain in the structurally complex aquatic habitats of the floodplain where water velocity is low (Winemiller, 1996). However, littoral patch habitats (e.g. woody snags) may be exposed and dry out as the flood waters recede to the main river. As a result, littoral fish species are forced to continually move and reassemble across the landscape in response to water levels. These patterns may result into a re-distribution of small fish communities on the floodplain (Hurtt & Pacala, 1995). The *species sorting model* predicts that community assemblage structure is a result of environmental heterogeneity, the habitat selection and environmental filtering that result from it (Hurtt & Pacala, 1995; Leibold et al., 2004). In the water environment, the interactions of both the physical and chemical properties equally play a significant role in determining fish species composition, distribution, abundance, movements and diversity (Leibold et al., 2004). Despite these environmental drivers in fish communities, no quantitative studies have been conducted to determine the response of small-sized and juveniles of the large growing fish communities to flood dynamics and water quality in the littoral zone of the Zambezi/Chobe floodplain. Therefore, the aim of this paper was to assess the influence of flooding phase and physicochemical parameters on the abundance and distribution of small-sized but matured and juveniles of the large growing fish communities in the littoral zone of the Zambezi/Chobe floodplain.

2 | MATERIAL AND METHODS

2.1 | Study area

The study was conducted on the Zambezi/Chobe floodplain located in Zambezi Region of Namibia. Based on the information available on Google satellite map, Zambezi Region is located at latitude 17°29′59.99″S and longitude 24°15′60.00″E. The region borders Botswana in the south, Angola and Zambia in the north, and Zimbabwe in the east (Simasiku & Mafwila, 2017). The Zambezi Region is home to two perennial rivers, namely the Kwando/Linyanti in the wet, and the Zambezi/Chobe in the east. Zambezi/Chobe is a highly pulsed and expansive river in terms of water volume during

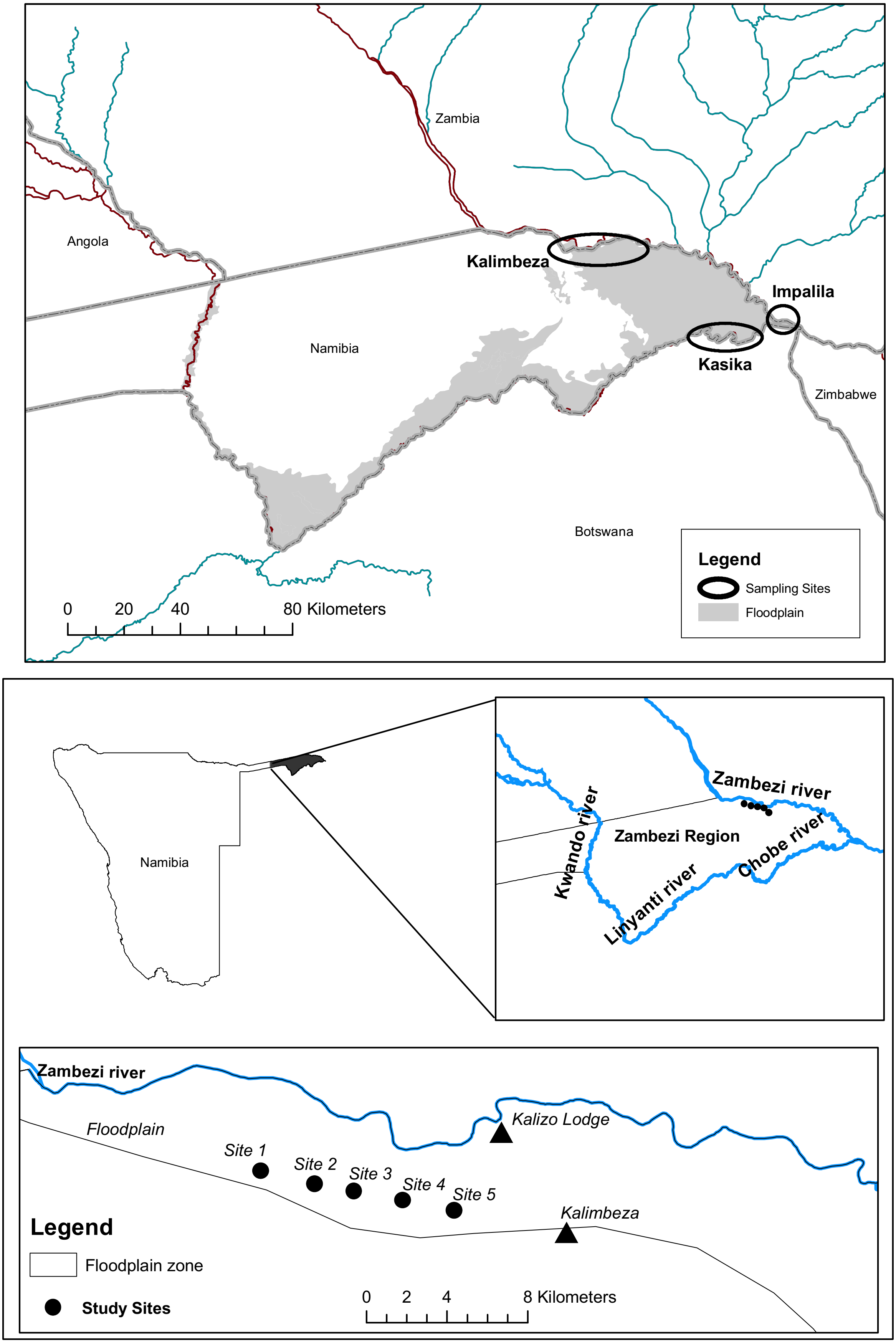

FIGURE 1 Map of the Zambezi region showing the location of Kalimbeza and the sampling sites along the littoral zone of the Zambezi/Chobe floodplain

the flooding season. The topography of the Zambezi Region is flat terrain with altitude ranging between 1,100 m in the west and 930 m in the east. Seasonal floodwater therefore transverses from the river catchments and spreads laterally by overflow, causing a large part in the eastern Zambezi Region to become one large floodplain (Hay et al., 2002; Mendelson & Roberts, 1997). The river usually reaches its peak between end of March and beginning of May after which the level recedes until the end of September. During the dry months (November–April), the aquatic habitat is reduced to a network of mud-bottom pools blanketed by *Salvinia* spp.

2.2 | Littoral survey schedule

Littoral surveys on the Zambezi/Chobe floodplain were conducted from March 2017 to February 2018 during the four hydrological stages of flooding: rising phase (February–March), peak phase (April), receding phase (May–June) and low phase (August–January). The littoral margins along the Zambezi/Chobe floodplain were sampled in the vicinity of Kalimbeza section of the Zambezi/Chobe River (Figure 1). This was found to be suitable on account of its accessible marginal zone which enabled long-term sampling over the entire study period. The physicochemical parameters of the water were measured in situ per site, just before fish sampling on each sampling day in order to gain some insight into the influence of water quality on the fish communities. Dissolved oxygen (mg/L), conductivity (µS/cm), pH and temperature (°C) were measured using a multi-function sensor HQ40d portable meter and the average per flooding phase computed. Data on daily water levels for the sampling period were obtained from the Hydrology Department, Ministry of Agriculture, Water and Forestry in the Zambezi region.

2.3 | Sampling for littoral fish species

A 20 m long × 1.5 m deep anchovy seine net with 5 mm stretched mesh size with a 1 m bunt was used to sample for the littoral ichthyofaunal. The net was laid out and hauled from a distance of 10 m offshore while fish were herded into the net by disturbing the vegetation or substratum that might have provided refuge. Hauls were conducted per sampling event as recommended by Siziba et al. (2011). As a result, five consecutive hauls at distinct sites were conducted per sampling event. Sampling sites were adjusted according to the water level. The catch per haul within a hauled distance of 10 m was used as an index of Catch Per Unit Effort (CPUE). This CPUE assumed that the seine efficiency remained uniform in all areas since there were no modifications to the net over time. After sorting by species, all specimens were measured to the nearest millimetre Total Length (TL) or Fork Length (FL), and weighed to the nearest gram (g). A sub-sample (20 individual per fish species) was measured when a large number of fish was caught and the rest of the fish were then counted and weighed according to species.

3 | DATA ANALYSES

3.1 | Species diversity

To describe the diversity of the assemblages for small fish among the different stages of flooding, ecological parameters such as species diversity were examined for each flooding water phase as species richness (S = number of species) and composite diversity, which integrates both richness and evenness (Shannon–Wiener H') (Pielou 1966). Species diversity based on species abundance data was calculated using the following formulae in Primer v6:

$$\text{Shannon} - \text{Wiener Index}\, H' = -\sum Pi * \log_e(Pi) \qquad (1)$$

where Pi is the proportion of individuals found in the ith species.

3.2 | Catch per unit effort

Monthly Catch per unit effort (CPUE) using the species abundance data was calculated for the four dominant species. Hence, Catch Per Unit Effort was calculated as:

$$\text{CPUE} = \text{C}_i/\text{E}_i \qquad (2)$$

where C_i is the catch of species i (in numbers) and E_i is the effort expended to obtain i. As a result, Catch Per Unit Effort was standardised to total number of fish/haul.

TABLE 1 Mean and standard deviation of the water physicochemical parameters grouped by flooding phase of the Zambezi/Chobe floodplain

Variable	Rising	Peak	Fall	Low	*p* value
Oxygen (mg/L)	4.3 ± 3.2^{a}	5.7 ± 1.0^{b}	5.6 ± 4.8^{bc}	4.3 ± 0.1^{a}	0.005^{*}
pH	6.4^{a}	7.9^{b}	7.4^{b}	6.8^{c}	0.001^{*}
Conductivity (µS/cm)	116 ± 1.7^{a}	43.2 ± 4.9^{b}	92.9 ± 21.3^{c}	100.3 ± 12.9^{a}	0.001^{*}
Temperature (°C)	26.4 ± 1.4^{a}	27.6 ± 1.1^{ab}	22.9 ± 1.2^{c}	26.5 ± 4.15^{a}	0.002^{*}

Note: Different letters denote significant differences (Tukey's test $p \leq 0.05$).

*Significant values.

TABLE 2 Species composition during the different flooding phases in the littoral zone of the Zambezi/Chobe floodplain between March 2017 and February 2018

	Rising		Peak		Fall		Low	
	No	%No	No	%No	No	%No	No	%No
Cyprinidae								
Enteromius afrovernayi	–	–	6	0.8	2	0.1	2	0.1
Enteromius bifrenatus	51	14.6	44	6.1	98	5.3	276	13.8
Enteromius eutaenia	–	–	–	–	1	0.1	–	–
Enteromius haasianus	17	4.9	4	0.6	64	3.5	84	4.2
Enteromius multilineatus	1	0.3	–	–	33	1.8	10	0.5
Enteromius paludinosus	53	15.2	28	3.9	434	23.6	398	19.8
Enteromius poechii	7	2	7	1	64	3.5	16	0.8
Enteromius radiatus	5	1.4	6	0.8	31	1.7	7	0.3
Enteromius unitaeniatus	–	–	–	–	1	0.1	–	–
Opsaridium zambezense	–	–	44	6.1	5	0.3	–	–
Labeo spp.	8	2.3	56	7.7	99	5.4	27	1.3
Characidae								
Brycinus lateralis	1	0.3	4	0.6	17	0.9	25	1.2
Rhabdalestes maunensis	54	15.5	15	2.1	89	4.8	396	19.7
Micralestes acutidens	–	–	36	5	41	2.2	–	–
Hydrocynus vittatus	–	–	2	0.3	–	–	–	–
Cichlidae								
Oreochromis andersonii	32	9.2	23	3.2	96	5.2	29	1.4
Oreochromis macrochir	–	–	5	0.7	1	0.1	3	0.1
Coptodon rendalli	15	4.3	138	19.1	93	5.1	55	2.7
Pharyngochromis acuticeps	–	–	148	20.5	29	1.6	8	0.4
Pseudocrenilabrus philander	11	3.2	28	3.9	202	11	103	5.1
Serranochromis macrocephalus	–	–	–	–	3	0.2	–	–
Tilapia ruweti	30	8.6	20	2.8	308	16.8	353	17.6
Tilapia sparrmanii	37	10.6	41	5.7	71	3.9	27	1.3
Tilapia spp.	11	3.2	9	1.2	-	0	-	-
Hemichromis elongatus	1	0.3	44	6.1	16	0.9	1	0
Poecilidae								
Micropanchax hutereaui	–	–	2	0.3	–	–	3	0.1
Micropanchax johnstoni	15	4.3	2	0.3	20	1.1	176	8.8
Micropanchax katangae	–	–	1	0.1	1	0.1	4	0.2
Anabantidae								
Ctenopoma multispine	–	–	9	1.2	12	0.7	3	0.1
Clariidae								
Clarias gariepinus	–	–	–	–	3	0.2	–	–
Schilbeidae								
Schilbe intermedius	–	–	1	0.1	2	0.1	–	–
Total	349		723		1,836		2,006	

3.3 | Statistical analysis

All data were first checked for normality and homogeneity of variance using Kolmogrov–Smirnov and Levene's test in SPSS v26. As environmental variables conformed to the assumptions of parametric tests, they were grouped by flooding stage (rising, peak, receding and low water phase) and subsequently compared using one-way Analysis of Variance (ANOVA) (Zar, 1984). The

TABLE 3 Percentage (in number) contribution of the most abundant fish families caught during the different flooding phases in the littoral zone of the Zambezi/Chobe floodplain between March 2017 and February 2018

Fish family	Rising	Peak	Fall	Low
Cyprinidae	40.7	27.0	45.3	40.9
Characidae	15.8	7.9	9.0	21.0
Cichlidae	39.3	63.1	44.6	28.9
Poecilidae	4.3	2.0	1.1	9.2

non-parametric test, Kruskal–Wallis, was applied to compare the species diversity indices among the hydro-periods. Significant associations at $p < 0.05$ were identified using the Bonferroni correction and Tukey's range test.

3.4 | Multivariate analysis

To describe the assemblages for small fish among the four stages of flooding, a cluster analysis (group average) employing the Bray–Curtis similarity index was performed on the standardised abundance values of species using the multivariate techniques in PRIMER *v6*: MDS and cluster analysis (Clarke & Warwick, 2001). The data were transformed by applying a fourth-root transformation prior to the cluster analysis to avoid overemphasis of the most abundant species (Clarke & Warwick, 2001). MDS ordination analysis was performed on the same data as the cluster analysis. Similarity percentage (SIMPER) was used to indicate the average contribution of each species density to the similarity (typifying species) and dissimilarity (discriminating species) between groups of samples (Clarke & Warwick, 1994, 2001). The SIMPER analysis was done on abundance data after a fourth-root transformation. The cluster group factors were chosen as A for peak flooding water phase and B for (rising, receding and low flooding water phase), as these groupings were identified by the cluster analysis and MDS. A Bray–Curtis similarity was chosen with a 90% cut for low contribution, to avoid some insignificant contributions. However, only the top ten species contributing most to the similarity and dissimilarity are shown in this study (Tables 5 and 6). Associations between the physicochemical parameters and fish CPUE data were explored using Redundancy analysis (RDA) using Canoco 5.

4 | RESULTS

4.1 | Physicochemical parameters of water

Dissolved oxygen varied significantly among the four stages of flooding (ANOVA, $df = 3$, $p = 0.005$), being highest during the peak flooding phase (5.7 ± 1.0 mg/L), followed by the falling phase (5.6 ± 4.8 mg/L), and lowest during the rising (4.3 ± 3.2 mg/L) and low flooding phases (4.3 ± 0.1 mg/L) (Table 1). Recorded pH values also differed significant among the different stages of flooding (ANOVA, $p = 0.001$). The highest pH of 7.9 was recorded during the peak flooding phase, followed by the falling phase (7.4), low phase (6.8) and lowest during the rising flooding phase (6.4). Similarly, water conductivity differed significantly among the stages of flooding (ANOVA, $p = 0.001$), being highest during the rising phase (116 ± 1.7 µS/cm), followed by the low phase (100.3 ± 12.9 µS/cm), falling flooding phase (92.9 ± 12.3 µS/cm) and lowest during the peak flooding phase (43.2 ± 4.9 µS/cm). Temperature also varied among the stages of flooding (ANOVA, $p = 0.002$), being highest during the peak flooding phase (27.6 ± 1.1°C), followed by the low phase (26.5 ± 4.15°C), rising phase (26.4 ± 1.4°C) and lowest during the falling flooding phase (22.9 ± 1.2°C) (Table 1).

4.2 | Catch compositions by flooding phase

A total of 4,914 individual fish representing 31 different species and seven families were recorded between March 2017 and February 2018 (Table 2). During the rising phase, 349 individual fish were collected, representing 17 species and the most numerous species were *Rhabdalestes maunensis* (15.5%), *Enteromius paludinosus* (15.2%) and *Enteromius bifrenatus* (14.6%). During the peak phase, 723 individual fish were collected, representing 27 species with *Pharyngochromis acuticeps* (20.5%) and *Coptodon rendalli* (19.1%) the most abundant species. During the receding phase, 1836 individual fish were collected, representing 28 species with *E. paludinosus* (23.6%), *Pseudocrenilabrus philander* (11.0%) and *Tilapia ruweti* (16.8%) accounting for most of the total catch. During the low phase, 2006 individual fish were collected, representing 23 species with *E. paludinosus* (19.8%), *R. maunensis* (19.7%) and *T. ruweti* (17.6%) the most abundant species (Table 2). Cichlids (63.1%) were more prevalent during the peak flooding phase while cyprinids (45.3%) were most abundant during the flood recession phase (Table 3). Fish species richness was significantly higher during the flood recession phase and lowest during the rising phase (Kruskal–Wallis test, $p < 0.001$) (Table 4). The Bonferroni correction for pairwise comparisons showed a significant difference between the rising phase versus low flooding phase. However, there was no difference in littoral species diversity and evenness among the flooding phases of the Zambezi/Chobe floodplain ($p > 0.05$) (Table 4).

4.3 | Fish assemblage structure in the littoral zone

A dendrogram and the non-metric multidimensional scaling (Figure 2a,b) showed distinct assemblages of fish caught among the four flooding phase (rising, peak, fall and low) of the Zambezi/Chobe floodplain. Aggregated fish catch composition by flooding phase was hierarchically grouped into two clusters. According to the SIMPER test results, catch composition was similar for Group B (fall, low and rising flooding phase), a cluster that is significantly different from Group A (peak flooding phase). From the SIMPER test results, the average similarity of Group B is 65.8%, and the similarity is more driven by the average abundance of *E. paludinosus*, *T. ruweti* and *Rhabdalestes maunensis* (Table 5). The average dissimilarity between Group A and B is 61.9% and mostly driven by *E. paludinosus*, *T. ruweti* and *R. maunensis* in Group B and *Pharyngochromis acuticeps*, *C. rendalli* and *Labeo* spp. in Group A (Table 6). SIMPROF results showed a significant difference in small fish assemblages between group A and B (*R* = 0.570; *p* = 0.001). The species that mostly contributed to this dissimilarity are *Pharyngochromis acuticeps*, *C. rendalli*, *E. paludinosus*, *T. ruweti*, *R. maunensis*, *O. zambezense*, *H. elongates*, *Labeo* spp., *Micropanchax johnstoni* and *Micralestes acutidens*. Among these species, juvenile *C. rendalli* is of commercial value in the area.

TABLE 4 Diversity, evenness and richness indices of small fish taxa sampled during the different flooding phases in the littoral zone of the Zambezi/ Chobe floodplain

Diversity indices	Rising	Peak	Fall	Low	*p* value
Species richness (S)	17^a	27^b	28^b	23^c	0.001*
Pielou's evenness (J′)	0.9	0.8	0.8	0.7	0.31
Shannon–Weiner (H)	2.5	2.5	2.5	2.3	0.11

Note: Different letters denote significant differences.
*Significant values.

4.4 | Correlation between physicochemical parameters and fish abundance

Redundancy analysis (RDA) based on fish abundance and the water's physicochemical parameters recorded during the different flooding phases yielded three pairs of redundancies across dissimilarity coefficients for canonical ordination of community composition, explaining 70.5% of variation in the dataset (Figure 3). Only three variables (water level, dissolved oxygen and conductivity) had a marked influence on small fish assemblages in the Zambezi/Chobe floodplain. The following species, *Enteromius multilineatus*, *Enteromius poechii*, *Enteromius*

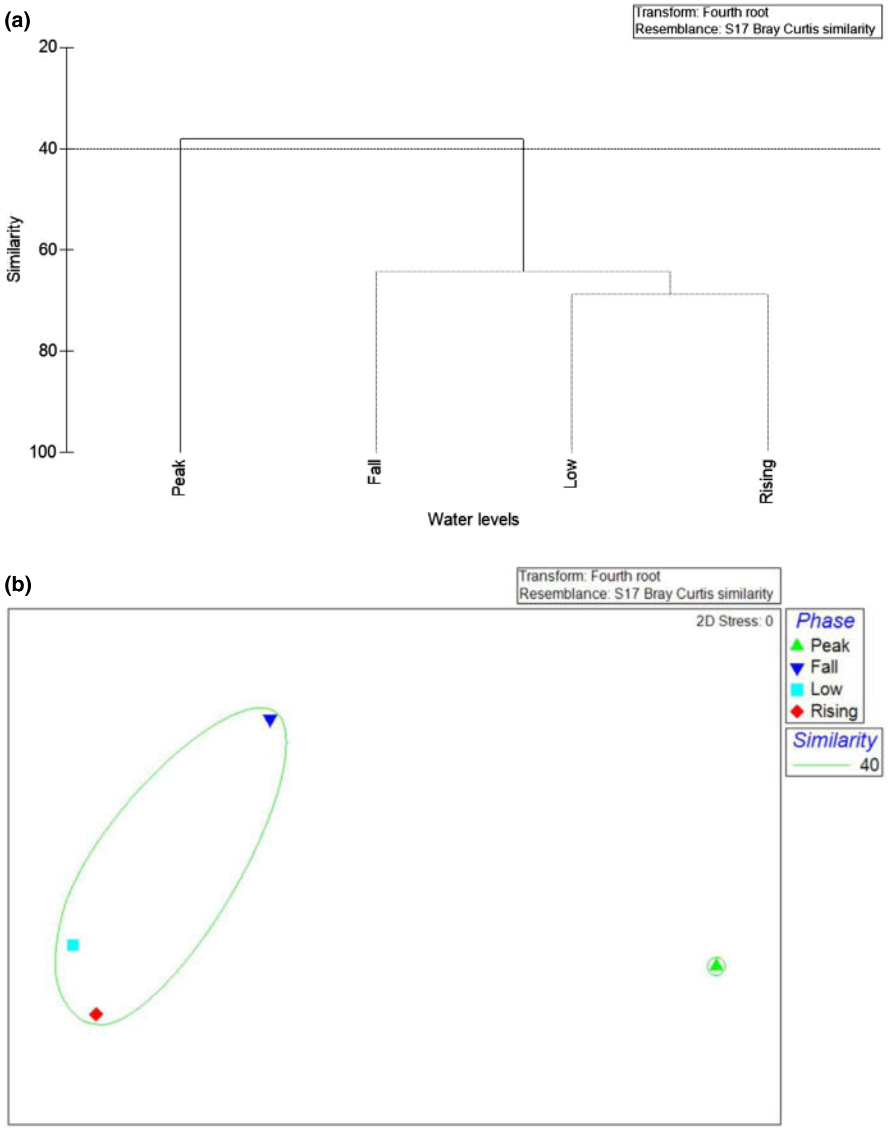

FIGURE 2 Dendrogram for hierarchical clustering analysis (a) and the multi-dimensional scaling (MDS) ordination (b) based on species richness grouped by hydro-periods (rising, peak, fall and low flooding phase) in the Zambezi/Chobe floodplain

haasianus, *P. philander* and *T. ruweti*, were inversely related to conductivity and positively related to dissolve oxygen concentration while *Micralestes acutidens* was inversely related to water level (Figure 3).

4.5 | Catch rates of the four most abundant species

Only four species, *Oreochromis andersonii*, *C. rendalli*, *T. ruweti* and *P. philander*, were collected in sufficient numbers (>10 individual) at different flooding phases to determine their response to a change in water level. Community structure of these four species in the littoral zone was interpreted from the monthly CPUE data. *Oreochromis andersonii* was more abundant in May 2017 (corresponding to the flood recession phase) while *C. rendalli* was abundant in April 2017 (peak flooding phase). These differences in CPUE between these two flooding phases were significant for both *O. andersonii* and *C. rendalli* (Mann–Whitney U test, $p < 0.001$). *Tilapia ruweti* and *P. philander* had a similar pattern observed for their monthly catch rates on the floodplain (Figure 4). The highest CPUE for both species was recorded in July (flood recession phase) and was least abundant from September 2017 to February 2018 (low flooding phase) (Figure 4). These differences were significant for both *T. ruweti* and *P. philander* (Kruskal–Wallis test, $df = 4$, $p < 0.001$).

4.6 | Length frequency of the four most abundant species

Oreochromis andersonii and *C. rendalli* are juveniles of the large growing species, whereas *T. ruweti* and *P. philander* are small-sized species that rarely grow to larger sizes, more than 130 mm TL. While there is limited information on maturity lengths of *T. ruweti* and *P. philander*, both species are reported to attain maturity at a length between 80 and 90 mm (TL) (Skelton, 2001) while the reported length at 50% maturity for *O. andersonii* is 240 mm (TL) and 214 mm (TL) for *C. rendalli* (Peel, 2012). Juvenile *O. andersonii* and *C. rendalli* (between 30 and 50 mm TL) were recorded during the rising phase in March 2017 (Figure 5) while larger specimens of both species (50–80 mm TL) were recorded during the flood recession phase (June 2017) (Figure 5). These differences in size between these two flood phases were significant for both *O. andersonii* and *C. rendalli* (Mann–Whitney U test, $p < 0.001$). Unlike *O. andersonii*

TABLE 5 SIMPER results showing the average similarity in littoral fish assemblages among the low, recession, and rising flooding phase of the Zambezi/Chobe floodplain

Species	Av.Abund	Av.Sim	Sim/*SD*	Contrib%	Cum.%
Enteromius paludinosus	0.18	15.97	6.8	24.25	24.25
Tilapia ruweti	0.14	11.06	2.36	16.8	41.05
Rhabdalestes maunensis	0.13	8.12	1.44	12.33	53.38
Enteromius bifrenatus	0.09	6.79	2.98	10.32	63.7
Pseudocrenilabrus philander	0.06	4.05	3.05	6.14	69.84
Enteromius haasianus	0.04	3.83	6.68	5.82	75.66
Coptodon rendalli	0.04	3.48	4.11	5.29	80.95
Oreochromis andersonii	0.05	2.87	1.29	4.35	85.31
Tilapia sparrmanii	0.05	2.32	1.57	3.53	88.84
Micropanchax johnstoni	0.05	2.25	1.16	3.41	92.25

TABLE 6 SIMPER results showing the average di-similarity in littoral fish assemblages between group A (peak flooding phase) and group B (low, recession, and rising flooding phase) of the Zambezi/Chobe floodplain

	Group A	Group B				
Species	Av. Abund	Av. Abund	Av. Diss	Diss/*SD*	Contrib%	Cum.%
Pharyngochromis acuticeps	0.2	0.01	10.08	21.26	16.28	16.28
Coptodon rendalli	0.19	0.04	7.56	13.17	12.21	28.49
Enteromius paludinosus	0.04	0.18	7.28	3.38	11.77	40.26
Tilapia ruweti	0.03	0.14	5.69	2.16	9.19	49.45
Rhabdalestes maunensis	0.02	0.13	5.45	1.42	8.81	58.26
Opsaridium zambezense	0.06	0	3.05	32.03	4.93	63.19
Hemichromis elongatus	0.06	0	2.89	12.84	4.67	67.86
Labeo spp.	0.08	0.03	2.4	2.23	3.87	71.73
Micropanchax johnstoni	0	0.05	2.31	1.14	3.73	75.46
Micralestes acutidens	0.05	0.01	2.16	3.23	3.48	78.94

and *C. rendalli*, the emergence of juvenile *T. ruweti* and *P. philander* between 40 and 50 mm (TL) was observed during the low flooding phase season in July 2017 (Figure 5). However, there were no clear patterns in seasonal mean size of *T. ruweti* and *P. philander* and their recruitment patterns were inconclusive in the Zambezi/Chobe floodplain. However, larger *P. philander* up to 55 mm TL and *T. ruweti* (60 mm TL) were observed during the low flooding phase (October 2017–January 2018) (Figure 5). These differences were significant for both *T. ruweti* (Kruskal–Wallis test, $df = 2$, $p < 0.001$) and *P. philander* (Kruskal–Wallis test, $df = 2$, $p = 0.024$).

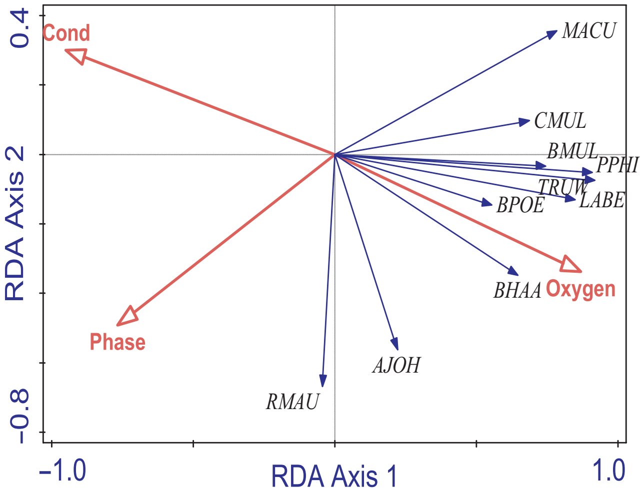

FIGURE 3 Redundancy analysis (RDA) of fish CPUE in the littoral zone of the Zambezi/Chobe floodplain and the three physicochemical variables (Cond = conductivity, Phase = water level phase and dissolved oxygen) collected in 2016/2017. RMAU = Rhabdalestes maunensis, AJOH = Micropanchax johnstoni, BHAA = Enteromius haasianus, BPOE = E. poechii, LABE = Labeo spp, TRUW = Tilapia ruweti, PPHI = Pseudocrenilabrus philander, BMUL = E. multilineatus, CMUL = Ctenopoma multispine, MACU = Micralestes acutidens

5 | DISCUSSION

The aim of this paper was to examine the influence of hydrological cycle and water quality on small-sized and juveniles of large growing fish assemblages and abundance patterns within the littoral zone of the Zambezi/Chobe floodplain. The current study found no significant difference in the littoral species diversity among the different flooding phases of the Zambezi/Chobe floodplain. Over 80 different fish species have been documented in the Upper Zambezi River (Tweddle et al., 2015), and only 31 species were sampled from the littoral zone of the Zambezi/Chobe floodplain. This is higher than the 24 species recorded by Simasiku and Mafwila (2017) in the littoral zone of the Kavango floodplain but lower than 38 species recorded by Siziba et al. (2011) from the temporary floodplains of the Okavango Delta. These variations may be attributed to the different aquatic habitats with distinct characteristics, sampling equipment, sampling design and effort employed by the various studies (Peel, 2012; Simasiku, 2014; Siziba et al., 2011). Three fish families

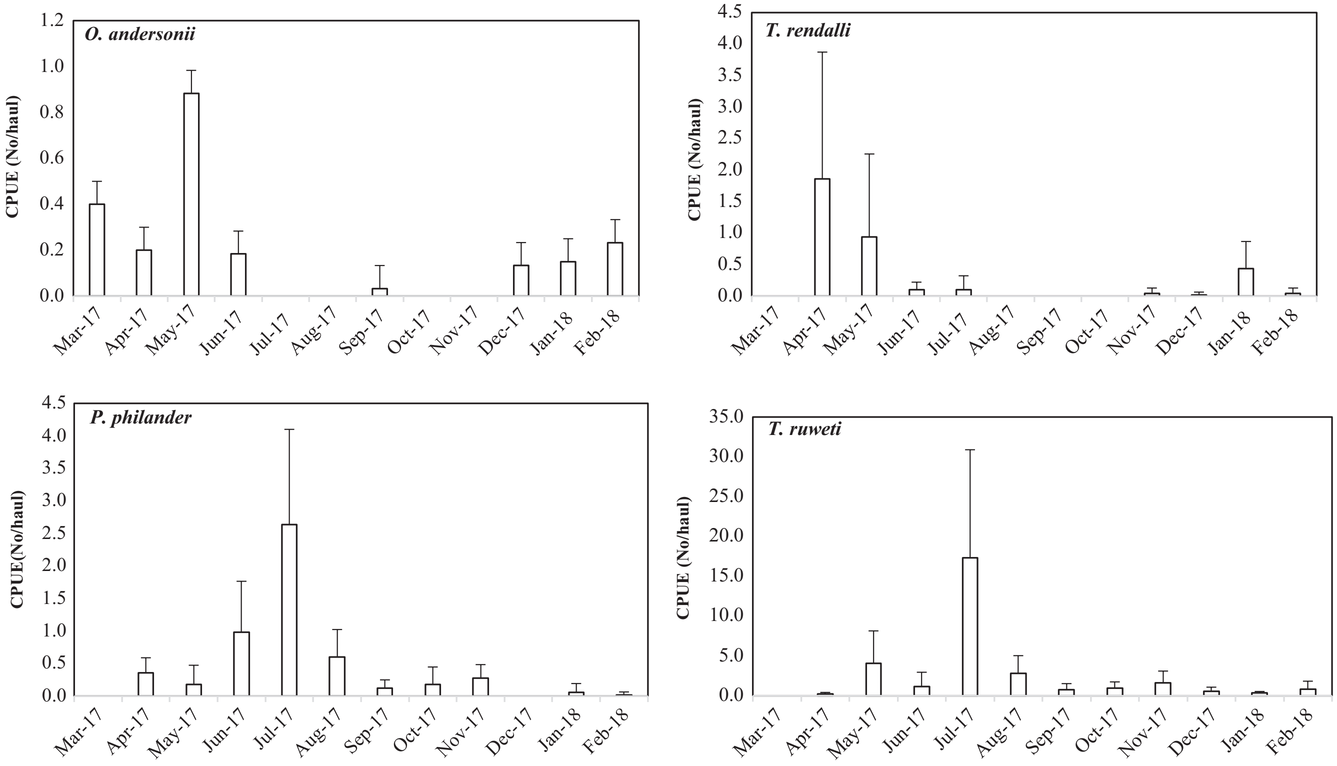

FIGURE 4 CPUE (in number) of *O. andersonii*, *C. rendalli*, *T. ruweti* and *P. philander* obtained during different months of the sampling within the littoral zone of the Zambezi/Chobe floodplain

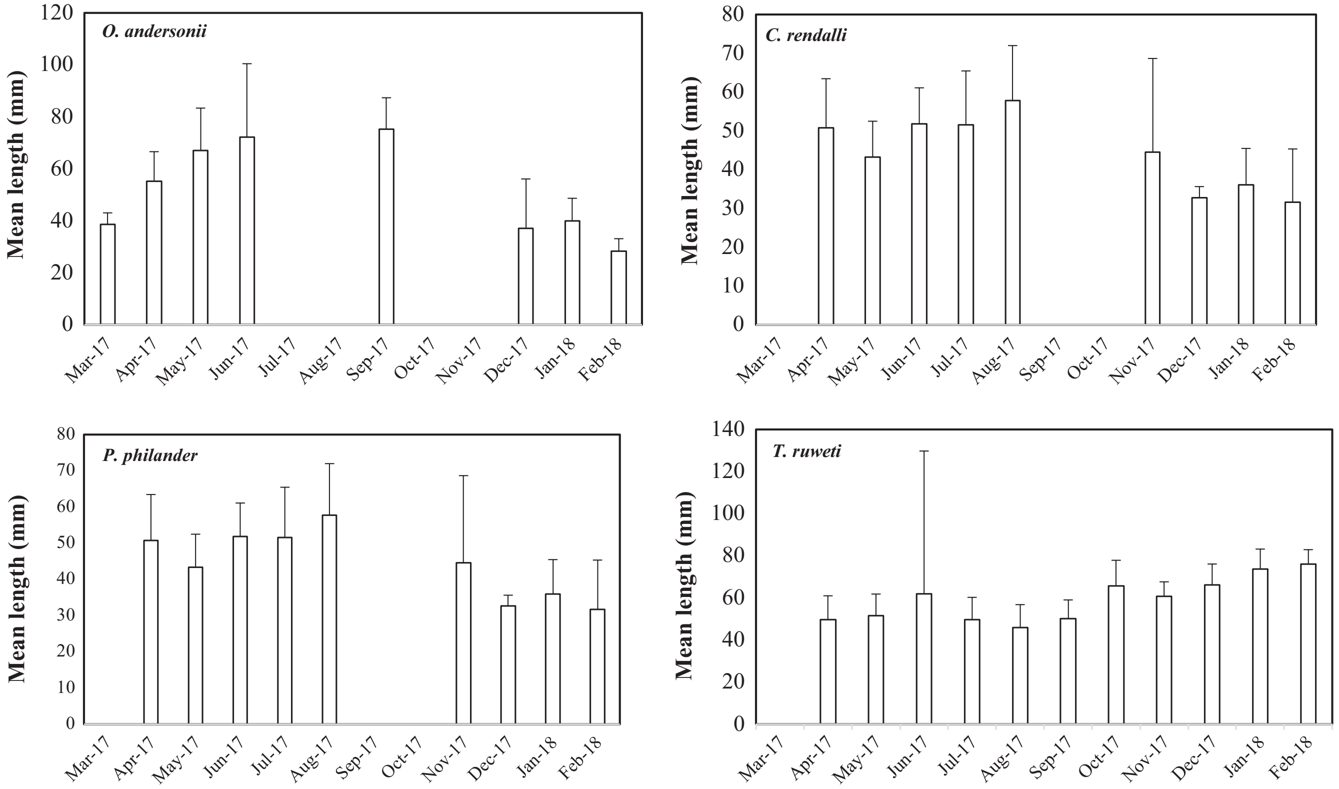

FIGURE 5 Mean size of *O. andersonii*, *C. rendalli*, *P. philander* and *T. ruweti* obtained during different months of the sampling within the Zambezi/Chobe floodplain

namely cichlids, characids and cyprinids dominated the catch in this study, accounting for more than 80% of the total catch (Table 2). The prevalence of these fish families in the littoral zone of the Zambezi/Chobe floodplain supports the studies of Høberg et al. (2002) and Siziba et al. (2011) who reported high incidence of juvenile cichlids and cyprinids within the temporary floodplains of the Okavango River. This high incidence of small fish has been reported as an 'ecological' adaptation (Jobling, 1995), such that during low flows, floodplains dehydrate and support terrestrial processes such as the growth of terrestrial flora and foraging by wildlife (Bonyongo, 2004; Ramberg et al., 2006). These terrestrial processes, together with the dead, decomposing macrophytes of the previous flooding season, make nutrients available during the inundation of encroaching flood waters which in turn support a large biomass of aquatic macrophytes (Junk et al., 1989). These aquatic macrophytes play a vital role in stabilising sediment and providing habitat diversity and shelter, substrata for periphyton and sites for abundant food production for invertebrates and fish (Howard-Williams, 1981; Machena, 1997; Pelican et al., 1978; Wetzel & Hough, 1973).

When the ichthyofaunal similarity by flooding phase was taken into account, two groups were identified: (a) peak flooding (b) fall, low and rising phase. Species composition differed significantly among these flooding phases. This is possibly related to specific flooding phase characteristics. The peak flooding phase exhibited a series of characteristics that distinguish it from the other stages of flooding such as high levels of dissolved oxygen, high water temperature, slightly alkaline pH and lower conductivity. There was a prolonged flood receding phase characterised by hostile environmental conditions such as high water temperatures, low dissolved oxygen and high conductivity. Hence, the observed variations in species composition among the different stages of flooding may further reflect the influence of water quality and food availability on the fish species. Higher densities of small fish (especially cichlids) were recorded during the peak flooding phase. Cichlid population tends to dominate in response to high water levels when aquatic hydrophytes had established (Siziba et al., 2011). High densities of zooplankton are known to develop soon after the flooding and these form an important source of food for juvenile fish (Siziba et al., 2011). As a result, these favourable feeding grounds might have attracted and accounted for the high abundance of cichlids and cyprinids onto the study floodplain. Similar findings on the prevalence of cichlids during peak water levels in the Kavango floodplain were reported by Hocutt and Johnson (2001). In contrast to cichlids, cyprinids were more prevalent during the low flooding stage; their dominance during this period may be allied by their high tolerance to harsher environmental conditions (Skelton, 2001). Cyprinids are reported to survive low dissolved oxygen condition, showing signs of suffocation only when the oxygen concentration is below 1.5–2.0 (mg/L) (Alabaster & Lloyd, 1980). This is lower than 4.3 and 5.7

(mg/L) recorded on the Zambezi/Chobe floodplain (Table 1 above). Similarly, Siziba et al. (2011) reported a dominance of cyprinids during the terminal phase of desiccation with low concentrations of oxygen in the Okavango delta. These observations are also confirmed by the species sorting model, stipulating that aquatic hypoxia during the dry season favour tolerant species such as cyprinids and poeciliids (Agostinho et al., 1997). Lower dissolved oxygen during the flood recession period as found in this study may have been attributed to the high rate of decomposition of organic matter, especially of aquatic plants origin covering the floodplain as reported by Miranda and Hodges (2000). Although, temperature is known to be a critical factor that influences both aquatic life and other physicochemical processes in the aquatic system (Mbalassa et al., 2014); the temperature and pH data from this study showed no relationship to the small fish community assemblages. Temperature is relatively constant in tropical streams and is therefore considered to be less of an influence on fish behaviour than in temperate catchments (Lowe-McConnell, 1987). Tropical species grow best at temperatures between 20 and 32°C (Lowe-McConnell, 1987) and the water temperatures recorded in this study (Table 1) remained within this range year-round. In a similar study, Leveque and Quensiere (1988) ranked water level and oxygen concentration among the most important factors affecting community structure in shallow lakes. Indeed, the flooding phase, dissolved oxygen and conductivity were the major factors noted to influence the fish community structure in this study.

On a species level, the abundance of *O. andersonii* and *C. rendalli* was highest in February–March (corresponding to the rising flooding phase) while *P. philander* and *T. ruweti* were most abundant in May–June (receding flooding phase). The observed abundance of *O. andersonii* and *C. rendalli* during the rising flood phase follows their biology, coinciding with their peak breeding periodicity from August to March (Peel, 2012; van der Waal, 1985). In Lake Chicamba, Mozambique, research also showed that high juvenile densities of *Oreochromis mossambicus* and *C. rendalli* coincided with the warm, wet season in March (Weyl & Hecht, 1998). Suitable water temperature, food availability and habitat complexity on the floodplain may have enhanced their spawning success and contributed to the increase in recruitment during the early flooding stage. By contrast, the abundance of *T. ruweti* and *P. philander* was observed outside their reported peak breeding season in September (Skelton, 2001). High densities of juvenile *T. ruweti* and *P. philander* during the flood recession indicate that the breeding pattern of these species is not restricted to flooding, and this corroborates the notion that breeding in cichlids is independent of flooding (Junk et al., 1989).

Individual fish densities of *O. andersonii*, *C. rendalli*, *T. ruweti* and *P. philander* were rapidly reduced to very low numbers as the floodwaters started to recede in August 2017–February 2018 and their habitats of choice became less available. One of the common behaviours in fish and other mobile animals is the ability to move away from unsuitable conditions (Siziba et al., 2011). Thus, juvenile *O. andersonii* and *C. rendalli* in this study left the littoral zone at an average size between 70 and 80 mm (TL) just before the connection with the main river channel was lost. During the flood recession phase, the floodplain habitat starts to shrink, and fish populations are expected to migrate to the main river stream (Chapman et al., 2000; Chapman & Kramer, 1991). Ellender et al. (2008) reported that juvenile *Oreochromis mossambicus* left the shallow marginal zone of the East Kleinemonde Estuary into open deep-water channels at an average size of 80 mm. In the Kavango floodplain, *O. andersonii* and *O. macrochir* left the marginal zone into the main river channel at an average size between 80 and 90 mm (TL) (Simasiku & Mafwila, 2017). Similarly, Jackson (1961) found that juvenile *O. macrochir* live along the swampy edge of Lake Mweru in Zambia and recruit into the open waters at a length greater than 80 mm when they are active enough to avoid predation by *H. vittatus*. These observations indicate that juvenile fish inhabit the littoral zone and only extend into the deeper main river channel at a size large enough to minimise predation pressure. The 'predator-prey wave' theory states that piscivorous predators target prey of specific size and that prey are relatively safe from predation once they are above that critical size (Savill & Hogeweg, 1999). Among other predators observed in this study, *Schilbe intermedius* and *Clarias gariepinus* were observed during the low flooding phase and may have contributed to a regulatory effect on small fish in this study. Similarly, a decline in juvenile densities of bluegill bream (*Lepomis macrochirus*) after a severe drawdown was ascribed to high predation pressure by largemouth bass (Hutchinson, 1953; Townsend, 1989). These observations reinforce the patch dynamics mode, emphasizing that less-competitive species are initially common during the flood pulse, and largely replaced by superior competitors as well as predators during the drawdown events (Hutchinson, 1953; Townsend, 1989).

6 | CONCLUSION

The extent of flooding and water quality (i.e. temperature, oxygen and conductivity) was the key determinant of the fish community structure in the littoral zone of the Zambezi/Chobe floodplain. Thus, with the various water developmental projects such as irrigation, hydropower dams, and the expansion of municipal water supplies being carried out in the catchment areas of Angola, Namibia and Botswana, pausing a threat of decreasing the water inflows into the Zambezi/Chobe River (Simasiku, 2014; Siziba et al., 2011). This might adversely affect fish recruitment and assemblage in the Zambezi/Chobe River. Moreover, the study area is prone to the impact of climate change, and therefore, these threats to the amount of water reaching the Zambezi/Chobe floodplain might negatively affect fish species, particularly the cichlids that rely heavily on the floodplains for feeding, nursing and recruitment. Cichlids are ecologically and economically important human food source in the Zambezi Region, and their decline will negatively affect trophic structures and livelihoods.

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CONFLICT OF INTEREST

We declare a close relationship between one of the editors for this respective journal; Mr Denis Tweddle and his review for this article might bias the content and findings of this article. For the sake of fairness and the outmost interest of this article and the target journal, it will be appreciated if other independent reviewers should be considered.

AUTHORS CONTRIBUTIONS

Dr. Evans Simasiku is the main author and initiator of the project, participated in data collection, data entry, data cleaning, writing up of the paper, with contributions to all sections of the paper. Dr. Clinton Hay supervised the initiation and facilitation of the project. He also conducted most multivariate statistical analyses of the project. Dr. James Abah participated in data collection, data entry, editing and critical shaping of scientific languages.

DATA AVAILABILITY STATEMENT

Derived data supporting the findings of this study are available from the corresponding author upon reasonable request. However, such data should be archived and only be shared at the discretion of the corresponding author.

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