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Natural hybridization between species of the cichlid genus *Oreochromis* (Cichlidae, Perciformes) in ponds of the low Ruzizi River (DR Congo)

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Abstract
Between 1948 and 1975, 3 species *Oreochromis niloticus*, *O. leucostictus* and *O. macrochir* were introduced into the Ruzizi plain, the natural distribution area of the subspecies *Oreochromis niloticus edouardianus*. Hybridization is observed between these species. The Mann-Whitney U test revealed significant differences between *O. niloticus* and its hybrids for the number of brachiospines; length of the last dorsal soft ray; and length of the lower jaw; *O. macrochir* differs from its hybrids in the number of branchiospines and length of the lower jaw; and *O. leucostictus* differs from its hybrids in the number of scales in the longitudinal line, the upper lateral line, the number of gill rakers, the length of the last dorsal soft ray, the length of the snout and the diameter of the eye. These characteristics are not sufficient to distinguish these three species from their hybrids without recourse to quality characteristics.

Keywords: Biological invasion, Ruzizi plain, hybrid, meristic, morphometry, native species

1. Introduction
Many publications on African waters report about 300 cases of fish transfer from one country to another, from one basin to another, or within a country or a basin [7, 10, 11, 24]. These transfers were for the purpose of obtaining fast-growing species, the reproduction of which can be easily controlled [3, 17, 22]. Low fertility and dwarfism, two problems encountered in farming of Tilapia and *Oreochromis* fishes, led to new transfers of some species of these two genera to obtain fast-growing monosexual hybrids [15, 19]. These introduced species influence their new environment, including closely related native species. One example is the natural and spontaneous hybridization between native and introduced species of the genera Tilapia and *Oreochromis* [11], or between species of the genus *Oreochromis* [8, 9, 12, 21, 23, 31].
The Ruzizi River flows from Lake Kivu to Lake Tanganyika in East-Africa, and is the border between DR Congo and Ruanda and, between DR Congo and Burundi (Figure 1). The basin of the Ruzizi belongs to the native range of *O. niloticus edouardianus*, which is endemic to Lake Kivu [24, 29]. Furthermore, *O. tanganicae*, a Tanganyika lacustrine endemic species, was found in a pond in the Ruzizi basin, far from its natural habitat [25]. Yet, the Ruzizi harbours three other *Oreochromis* species: *O. macrochir*, *O. leucostictus* and *O. niloticus niloticus*, these species were introduced between 1948 and 1975 while transiting through Rwanda, Burundi and DR Congo. The natural distribution of *O. niloticus* covers Lake Tana, Edward, Gandjule, Abia, Rodolphe, Baringo, Albert and Chad, the rivers Chari, Bénoué, Niger, Volta, Nile, and Senegal. The species is known as endemic to Lake Kivu under the name *O. niloticus* edouardianus. *O. leucostictus* is naturally distributed in Lake Albert, Lake Edward, Lake George and tributaries [24]. Finally, *O. macrochir* naturally occurs in Lake Moero, Bangweulu, part of Katanga, Upper Kafue, Okavango River and Cunene [24]. The presence of related native and introduced species and subspecies in the same basin calls for an investigation of species integrity. Have the introduced species in the Ruzizi basin remained reproductively isolated from each other and the native subspecies? Natural hybridization among *Oreochromis* fishes has been commonly observed, including in Lake Naivacha [9], Katingiri [12], Bunyoni [21], Victoria [31] and Itasy [23]. The present work aims at verifying the presence of hybrids, and at comparing their morphological characteristics with those of the parental species.

2. Material and Method

2.1 Sampling area

Between 2016 and 2019, sample collection took place in permanent ponds in Nyangara (03º20.413S; 029º11.705'E); Mwaba (03º10.334 'S; 029º13.290' E.) and Kindava (03º05.558 'S; 029º14.777' E) in the Ruzizi plain (Figure 1). The choice of sites was based on the permanence of the waters, the importance of the fishing activity of fishes of the genus *Oreochromis* in the ponds, their proximity to the agglomerations and their accessibility.

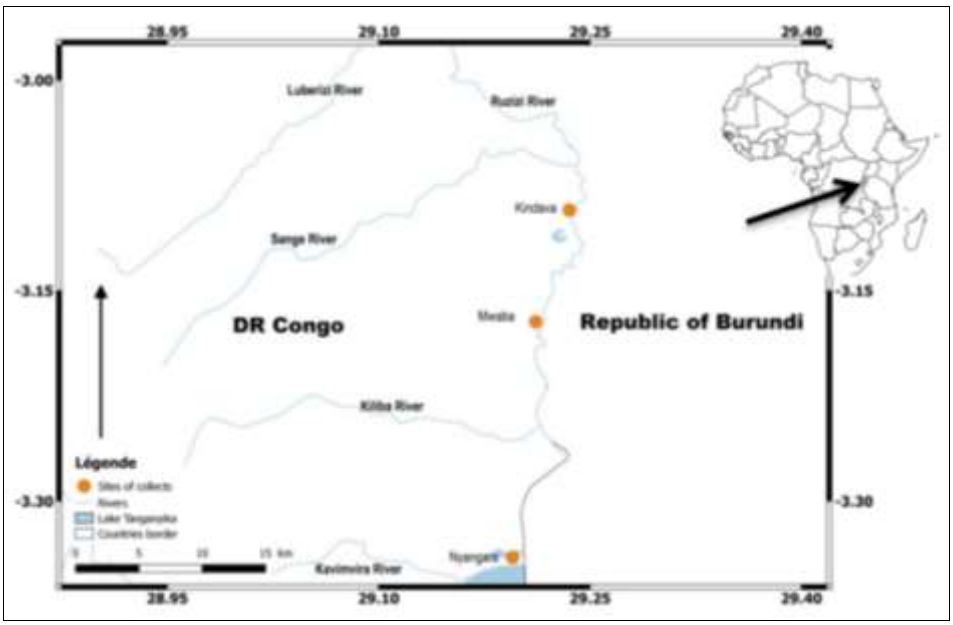


Fig 1: Sampling sites of *Oreochromis* specimens in the basin of the Ruzizi River (DR Congo)

2.2 Sampling gear

In the field, various types of fishing gear were used, such as beach seines, gill nets, fish traps and hooks. Fishing was practiced during the day and the night and; sometimes hand-catching was also practiced at around 4 am by local fishermen. A total of 113 specimens with the size from 46.9 to 160.4 mm in standard length (SL) were collected during 24 visits. Pictures of fresh fish specimens were taken to fix qualitative traits such as flank color and spots on the head, flank or fins. Collected specimens were labeled, kept in plastic bags and fixed with 10% formalin.

2.3 Species identification

Species identification was done according to Barrel *et al.* (1977) [4]. Specifically, *O. niloticus* was distinguished from *O. leucostictus* and *O. macrochir* based on meristics, morphometric and qualitative characters such as numerus caudal vertical bands vs. presence of spots on dorsal caudal and anal fin for *O. leucostictus* or no spots nor bands on fins of *O macrochir*, and hybrids were identified based on presence at once of specific distinctive qualitative characters of two species on a specimen (Figure 4: b, d, f). Subsequently, the following traits were quantified for all individuals: the number of fin rays; the pre-dorsal length; the length of the base of the dorsal and anal fin; the length of the upper and lower jaw according to Hubbs and Lagler (1958) [14]; and the number of scales on the upper and lower lateral line (including only the perforated scales). Furthermore, the innermost and outermost soft ray of the pelvic bone was measured from the base to the end.

2.4 Data analysis

All analyses were performed in Statistica for Windows, version 8. Meristic and measurement data were analyzed separately, and the measurements were log-transformed prior to the analysis. Meristic traits were first analysed using a Principal Component Analysis (PCA).

Subsequently, non-parametric Mann-Whitney U tests were performed to compare each trait separately for each species pair. P-values of these tests were corrected for multiple testing using a sequential Bonferroni correction. The metric traits were analysed in the same way as the meristic traits.

3. Results

The total sample included specimens of *O. leucostictus* (N = 20), *O. niloticus* (N = 46), *O. macrochir* (N = 5), *O. macrochir* x *O. leucostictus* (N = 6), and *O. niloticus* x *O. leucostictus* (N = 25). No specimens were classified as *O. niloticus* x *O. macrochir*.

3.1 Meristic analysis

A first PCR was performed with 7 meristics (n = 102). The most important values for PCI are the number of longitudinal scales and those of the lower lateral line. For PCII, the number of scales of the upper lateral line and the number of gill-rakers are important, and for PCIII the number of dorsal and pectoral fin rays (Table 1). The different groups have significant overlaps with PCI and PCII and do not allow a clear separation (Figure 2), although PCI values for *O. niloticus* were clearly lower than for *O. leucostictus*.

Table 1: Variable score for the first three axes of PCA obtained with 7 meristics taken from all the specimens observed (n = 113). The most important values are in bold.

Characters	PCI	PCII	PCIII
Dorsal spines	-0.163669	-0.000006	0.122942
Dorsal rays	-0.224630	-0.223112	0.490469
Pectoral rays	-0.093119	0.271495	-0.587296
Longitudinal scales	-0.437704	0.116599	0.238626
Upper lateral line	-0.254334	0.527054	-0.065821
Lower lateral line	-0.337632	-0.278819	0.389192
Gill rakers	0.116791	0.566052	0.292200

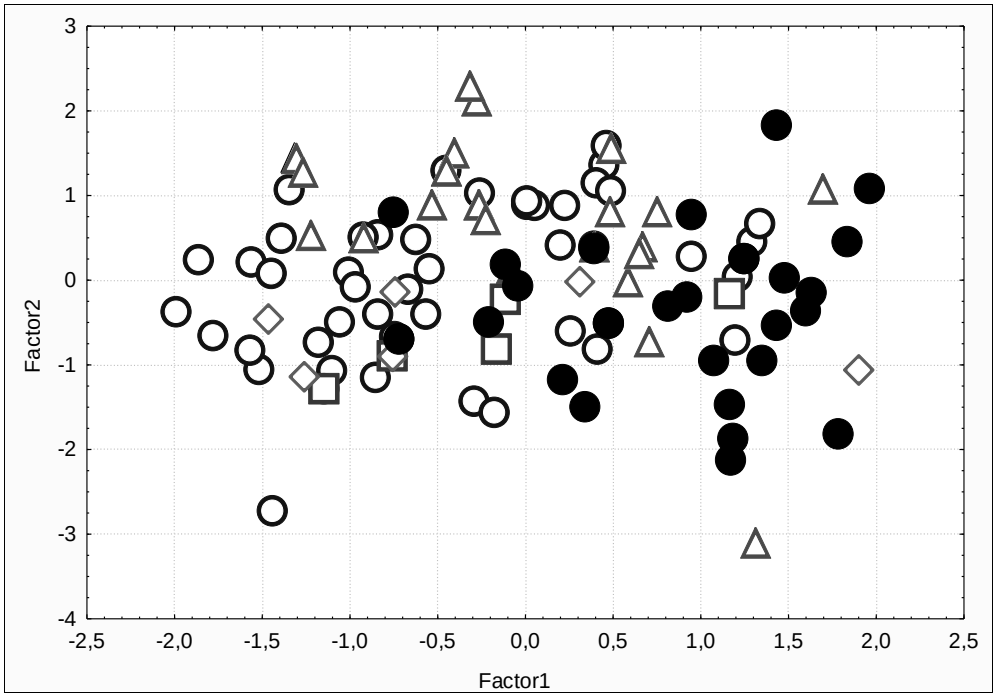


Fig 2: Scatterplot of PCI versus PCII obtained with data from 7 meristics ●: *O. leucostictus*, ○: *O. niloticus*, □: *O. macrochir*, ◇: Hybride *O. macrochir* x *O. leucostictus*, Δ: Hybride *O. niloticus* x *O. leucostictus*.

Mann-Whitney U-tests reveal significant meristic differences between *O. niloticus* and *O. leucostictus* for the number of dorsal spines, the number of longitudinal scales and that of the upper lateral line (Table 2); a significant meristic difference concerning the number of gill between *O. niloticus* and the *O. niloticus* x *O. leucostictus* hybrid; between *O. macrochir* and the hybrid *O. niloticus* x *O. leucostictus*. And finally, between *O. leucostictus* and the hybrid *O. niloticus* x *O. leucostictus* for the number of longitudinal scales, the upper lateral line scales and the number of gill rakers (Table 2).

Table 2: P-value for the Mann-Whitney U test between 5 groups including 3 species and 2 hybrids for 7 meristic traits. Significant P-values after sequential Bonferroni correction are marked in bold (H = hybrid).

Characters	***O. niloticus* vs. *O. macrochir***	***O. niloticus* vs. *O. leucostictus***	***O. macrochir* vs. *O. leucostictus***	***O. niloticus* vs. *H. macr-leu***	***O. niloticus* vs. *H. nilo-leu***	***O. macrochir* vs. *H. macr-leu***	***O. macrochir* vs. *H. nilo-leu***	***O. leucostictus* vs. *H. macr-leu***	***O. leucstictus* vs. *H. nilo-leu***
Dorsal spines	0.457902	0.000746	0.081439	0.123230	0.024947	0.173569	0.146427	0.442423	0.177267
Dorsal rays	0.681958	0.001365	0.013472	0.262804	0.005421	0.312871	0.031120	0.695484	0.879466
Pectoral rays	0.809021	0.429383	0.581501	0.107565	0.365179	0.173569	0.422679	0.391585	0.956596
Longitudinal scales	0.324885	0.000013	0.104044	0.773484	0.704730	0.382848	0.435233	0.016191	0.000216
Upper lateral line	0.212675	0.000290	0.291604	0.908267	0.299665	0.420740	0.083216	0.054596	0.000266
Lower lateral line	0.744720	0.034908	0.494952	0.887891	0.090830	0.701029	0.926296	0.238042	0.426028
Gill rakers	0.020772	0.932366	0.021654	0.016023	0.000121	0.571375	0.000905	0.011573	0.000369

3.2 Metric analysis

A second PCA was performed with 20 measurements on 113 specimens. Variables with a significant differences were individually plotted against SL. The most important values for PCI are the length of the snout, the dorsal longest soft ray length, and the inter-orbital width, and the most important for PCII, the eye diameter and the eye length are important, and for PCIII, the body depth, the head length and the longest anal ray length (Table 3). *O. niloticus* and *O. macrochir* were characterized by positive values for PCI, whereas PCI values for *O. leucostictus* were negative. The hybrids occupied intermediate position (Figure 3).

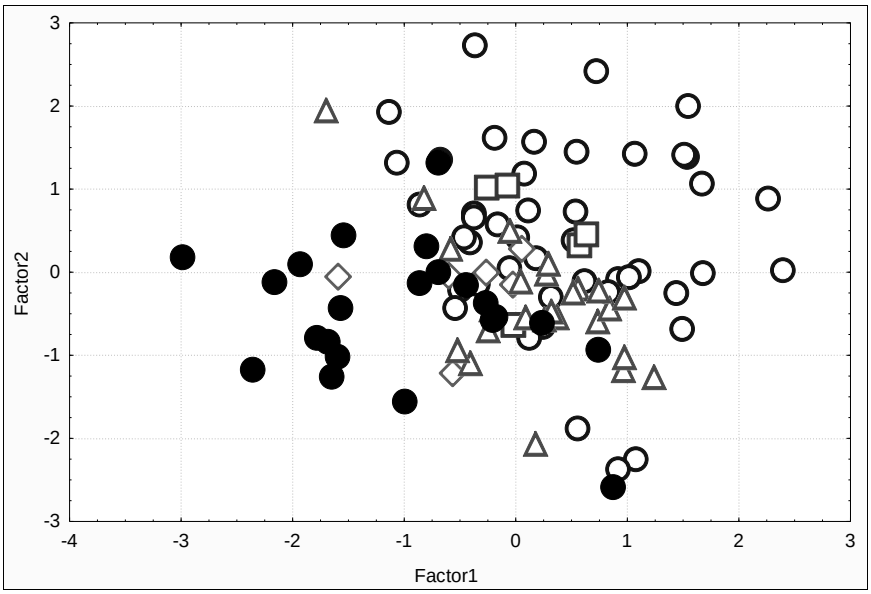


Fig 3: Scatterplot of PCII against PCIII obtained with the data of the 20 measures included in the PCA ●: *O. leucostictus*, ○: *O. niloticus*, □: *O. macrochir*, ◇: Hybride *O. macrochir* x *O. leucostictus*, Δ: Hybride *O. niloticus* x *O. leucostictus*.

Table 3: Variable scores for the first three axes of the PCA obtained with 20 measurements taken from all the specimens observed (n = 113). The most important values are in bold.

Characters	F1	F2	F3
% SL			
Body depth	-0.087496	-0.001874	0.257736
Head length	0.132416	-0.121101	0.286088
Caudal peduncle length	0.045542	-0.074730	0.074165
Caudal peduncle depth	-0.057577	0.056667	0.033707
Predorsal length	0.070852	-0.001797	-0.106956
Dorsal fin base length	-0.076005	0.182993	0.130276
Pectoral (in)	-0.095592	0.017517	0.110233
Pectoral (out)	-0.100253	0.100842	0.130603
Anal base length	-0.083496	0.112689	-0.138271
Longest dorsal spine length	-0.087492	0.133519	-0.043175
Longest dorsal ray length	-0.209555	-0.143031	-0.059678
Longest anal spine length	-0.031829	0.176430	0.198697
Longest anal ray length	-0.124617	0.101405	0.233940
% HL			
Snout length	-0.247954	-0.104870	0.006222
Eye length	-0.005962	0.325239	-0.056245
Eye diameter	0.090110	0.325605	-0.106287
Inter orbital width	-0.195526	-0.017403	-0.000014
Upper jaw length	-0.125236	0.070631	-0.169135
Lower jaw length	-0.041590	0.059477	0.201192
Cheek depth	-0.225219	-0.054204	-0.132688

Mann-Whitney U tests reveal 3 highly significant differences in measurements between *O. niloticus* and *O. leucostictus* for the length of the longest dorsal ray, the diameter of the eye and snout length. Furthermore, two measurements differ between *O. niloticus* and the hybrid of *O. niloticus* x *O. leucostictus*; the length of the longest dorsal ray and the length of the lower jaw. Finally, *O. leucostictus* differs from the *O. niloticus* x *O. leucostictus* hybrid for five measurements, most notably in snouth (Table 4).

Table 4: P value for the Mann-Whitney U tests between 5 groups including 3 species and 2 hybrids for 20 measurements. Significant P-values after sequential Bonferroni correction are marked in bold.

Characters	***O. niloticus* vs. *O. macrochir***	***O. niloticus* vs. *O. leucostictus***	***O. macrochir* vs. *O. leucostictus***	***O. niloticus* vs. *H. macr-leu***	***O. niloticus* vs. *H. nilo-leuco***	***O. macrochir* vs. H. mac-leu**	***O. macrochir* vs. *H. nilo-leuco***	***O. leucostictus* vs. *H. mac-leu***	***O. leucostictus* vs. *H. nilo-leuco***
% LS									
Body depth	0.662428	0.209477	0.288637	0.334664	0.354756	0.273323	0.253955	0.050041	0.009888
Head length	0.213127	0.186248	0.052993	0.747765	0.222627	0.361311	0.845573	0.197833	0.028095
Caudal peduncle length	0.616202	0.045213	0.080512	0.558746	0.830159	0.855132	0.388383	0.313548	0.105163
Caudal peduncle	0.264567	0.602580	0.151108	0.770017	0.136428	0.067890	0.676412	0.866609	0.092127

depth									
Predorsal distance	0.987100	0.009229	0.151108	0.003800	0.858938	0.028460	0.977802	0.197833	0.020132
Dorsal fin base length	0.391468	0.006457	0.662161	0.558746	0.830159	0.583883	0.303245	0.197833	0.005224
Pelvic (in)	0.528307	0.054536	0.802839	0.380456	0.956014	1.000000	0.559011	0.955350	0.069955
Pelvic (out)	0.046725	0.002665	0.900652	0.061338	0.218013	0.855132	0.027941	0.695114	0.001607
Base de l'anale	0.52837	0.061601	0.802839	0.095633	0.394290	0.583883	0.597040	0.910841	0.088082
Longest dorsal spine length	0.077991	0.169080	0.020917	0.04683	0.096749	1.000000	0.253955	0.050041	0.007225
Longest dorsal ray length	0.373844	0.000000	0.014920	0.015245	0.000046	0.067890	0.036905	0.239686	0.000756
Longest anal spine length	0.356719	0.092522	0.492331	0.084550	0.007403	0.715001	0.676412	0.822791	0.267585
Longest anal ray length	0.017462	0.089963	0.028915	0.334664	0.619606	0.044611	0.001132	0.614330	0.000435
% HL									
Snout length	0.616202	0.000002	0.014920	0.016517	0.262068	0.201244	0.889354	0.537973	0.000014
Eye length	0.159515	0.024898	0.001171	0.725721	0.018915	0.067890	0.004950	0.130609	0.864569
Eye diameter	0.507375	0.000001	0.028915	0.053666	0.066889	0.465209	0.717564	0.043841	0.000011
Interorbital width	0.169328	0.004275	0.0950229	0.0020913	0.014174	0.855132	0.522199	0.910841	0.468525
Upper jaw length	0.340098	0.621312	0.235640	0.429907	0.577053	0.100349	0.486675	0.695114	0.405702
Lower jaw length	0.029050	0.059767	0.000750	0.639953	0.000019	0.201244	0.000505	0.179033	0.000699
Cheek depth	0.884293	0.003457	0.061130	0.151994	0.094312	0.201244	0.231523	0.370345	0.135591

3.3 Qualitative characters

Oreochromis niloticu

At all stages of life, the caudal fin is marked by numerous vertical bands. The male is bluish-pink at times with a throat, ventral, anal and pelvic fins dark. The female is often dull white silvery brown with about 10 vertical bars [13], Figure 4. (a) and (g).

Oreochromis macrochir

The male has a dark green body with a green-cream ventral flank, red margin of the caudal fin and a long (> 25mm) genital papilla and truncated caudal fin in adults.

The female has an olive green body. Adults have green-dark heads, a blue-green snout, and dark spots on the temporal area (the gill cover and around the eye) [13], Figure 4(c).

Oreochromis leucostictus

The male is black with prominent white spots on the flanks and fins. The female is olive with the pale ventral region and unclear vertical bars, anal and caudal fins are dark [13], Figure 4(e).

O. noloticus* x *O. macrochir hybrid

The specimen has the typical bluish-pink colour of *O. niloticus* however the caudal fin is truncated and does not carry vertical streaks. It is dark as is the pectoral fin like that of *O. macrochir* Figure 4(b).

***O. macrochir* x *O. leucostictus* hybrid**

The specimen has clear spots on the dark flank and fins typical for *O. leucostictus*, however, the caudal is truncated, the olive color of females *O. macrochir* remains perceptible and dark spots on the gill cover are present Figure 4(d).

***O. leucostictus* x *O. niloticus* hybrid**

The specimen has typical dark spots on the flank and fins typical for *O. leucostictus* and a red caudal fin with vertical streaks and the typical reddish pectoral of *O. niloticus* Figure 4(f).

Hybrids from the same parent species do not exhibit the same meristic, morphometric, or color patterns. They present in different proportions mixtures of the pure parent characters; from which it is not possible to give them a precise diagnosis. This depends on the level of hybridization (F1: First Filiation, F2: Second Filiation and backcross)

a. *O. niloticus niloticus*

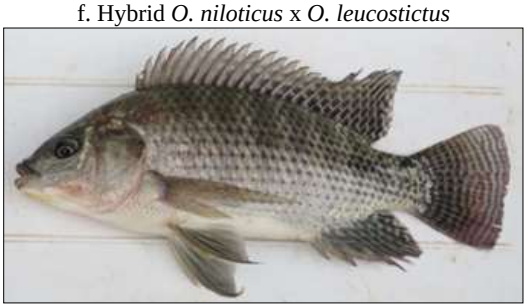
b. Hybrid *O. niloticus* x *O. macrochir*

c. *O. macrochir*

d. Hybrid *O. macrochir* x *O. leucostictus*

e. *O. leucostictus*

f. Hybrid *O. niloticus* x *O. leucostictus*



g. *O. niloticus edourdianus*

Fig 4: Species of the genus *Oreochromis* collected in the Ruzizi plain and their hybrids

4. Discussion

From the above results, it appears that hybridization occurs between three different species of the genus *Oreochromis* present in the lower Ruzizi: *O. niloticus*, *O. leucostictus* and *O. macrochir*. The hybrids present intermediate morphological characters between the parents species or close to one of them. As far as spots and coloration are concerned, the hybrids present both the characters of the two parent species. Interspecific hybridization is widespread in fish [15, 27]. It is more common in fish than in other vertebrate groups [1, 5]. It is often associated with human disturbance of populations or habitats where parental species were found. Four factors are considered likely causes of hybridization: habitat loss, expansion of the distribution range, aquaculture, and introduction. From 1950, *T. rendalli*, *O. macrochir* (first the Luapula–Mweru strain and later the Kafue River strain) have been introduced for fish culture purposes around Lake Kivu. These have escaped and are now established in the Lake. There has been some hybridization between *O. niloticus* edouardianus and *O. macrochir* in the Lake such that it is now not possible to assign some specimens to one or the other of those species [20]. Habitat destruction increases competition with fish species in close proximity to spawning habitat where breeding activities overlap, resulting in natural hybridization [18]. This phenomenon is particularly common when populations invade a new environment and overlap temporally and spatially in spawning activities [30, 32]. This trend is further reinforced by anthropogenic factors, such as habitat destruction, which increases competition for spawning habitat [2].

Deines *et al*. (2014) [6] observed significant differences in meristic traits between *O. niloticus* x *O. andersonii* hybrids and parental individuals. These variations include the number of scales in the upper lateral line, the number of soft rays of the anal fin, the number of scales in the lower lateral line, the number of scales between the anal fin and the upper lateral line, the scales around the caudal peduncle and the number of soft rays of the dorsal fin. For the morphometric characters, the most significant variations concerned length of the premaxillary pedicel, width of the lower jaw, length of the caudal peduncle, vertical diameter of the eye/long eye, horizontal diameter of the eye/depth of the eye and length of the base of the anal fin.

Quantifiable morphometric and meristic measurements do not distinguish hybrids *O. niloticus* x *O. andersonii* from parental individuals. Thus, when genetic analysis is not possible, future hybridization studies will need to continue to rely on color models to identify hybrids, recognizing that not all hybrids and backcrosses have the same color patterns [6]. Examining body shape variables and external body characteristics has the potential for misidentification in visual assessment [26].

The result of this study confirms earlier results obtained by Lowe Mc-Connel, 1982 [20] and Kim & al, 2001 [18], Wheeler, 1969 [32]; & Toscano, 2010 [30] which justify the hybridization of species of the genus *Oreochromis* by the loss of habitats, the introduction of species and aquaculture. In the lower Ruzizi, wetlands are subdivided or drained to make way for market gardening, and the three introduced species of the genus *Oreochromis* are found together in the same habitats as *O. niloticus* edoudianus after escaping from fishponds.

5. Conclusion

The protection of wetland habitats is necessary for the conservation of species. It is important to take into account the natural distribution of the species before proceeding with new introductions. There is competition in low Ruzizi for living space between the three introduced species of the genus *Oreochromis* on the one hand, and between these species and their hybrids on the other. The native subspecies *O. niloticus* edouardianus typical of the low Ruzizi is invaded by these three species and their hybrids. The chance of it supplanting them is minimal.

6. Acknowledgments

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