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Comparative Analysis of Morphometric and Meristic Characters in Oreochromis niloticus (Linnaeus, 1758), Nile Tilapia across Diverse Ecological Zones in Nigeria

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Authors' contributions

This work was carried out in collaboration among all authors. Authors AHA and SOA designed the study and wrote the first draft of the manuscript. Authors AHA, KM and ITA collected the samples for the study. Authors AHA, KM, ITA and SOA managed the literatures searches. Author AHA managed the analyses of the study and performed the statistical analysis. All authors read and approved the final manuscript.

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Original Research Article

ABSTRACT

The present study investigated the comparative analysis of morphometric and meristic characteristics in *Oreochromis niloticus* (Linnaeus, 1758) from six lakes in different ecological zones across Nigeria. A total of 347 samples were collected. Twenty-nine morphometric characters

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were measured to the nearest 0.01 cm using Vernier calipers and nine meristic characters were counted in all the collected individuals. The results of the univariate analysis of variance (ANOVA) revealed that all observed morphometric and meristic characters were significantly different (P=0.05) across the study sites. Notably, O. niloticus from Asejire Lake had significantly higher values in all the morphometric characters. The multivariate analysis of variance (MANOVA) identified three morphometric and four meristic characters as the most discriminating traits among the studied populations. These findings align with previous research highlighting the utility of morphometric and meristic data in delineating fish populations based on habitat differences and genetic compositions. Significant differences in head-related (head length), swimming-related (anal fin length and caudal peduncle length), and feeding-related (both left and right gill raker) measurements further underscored environmental influences on morphological variation. The study suggests that ecological factors such as food availability and environmental conditions contribute to the observed variations. This research provides valuable insights into the population dynamics and adaptation strategies of O. niloticus in diverse aquatic environments across Nigeria

Keywords: Comparative analysis; morphometric character; MERISTIC character; ecological zones; Nile tilapia.

1. INTRODUCTION

African cichlids are widely studied for their evolutionary processes, particularly due to their rapid speciation rates, adaptive radiations, and diverse speciation mechanisms [1-3]. Tilapia, a significant species in aquaculture both in Africa and globally, comprises three genera; Oreochromis, Sarotherodon, and Tilapia, within the Cichlidae family. These species, originally from Africa, are now globally distributed and have significant ecological and economic roles in their native habitats [4,5].

Over time. African cichlids have adapted to various aeographical areas. displaving phenotypic variations linked to their habitats [6]. phenotypic Analyzing variations through morphometric and meristic characters is a common method to differentiate fish stocks, as these characters respond to environmental changes differently across species. Such measurements provide valuable data for taxonomic classification [7]. Recognizing morphometric and meristic differences is crucial evaluating population structures for and identifying stocks as documented by different authors [8-16]. Morphomeristic studies are essential not only for taxonomy but also for understanding species health and reproduction [17].

In Nigeria, only few studies have been done on the comparative morphometric differentiation of Tilapia species such as *Tilapia zillii*, *Sarotherodon species*, and *Oreochromis niloticus* across different ecological zones. This research aims to compare the morphometric and meristic characters of *O. niloticus* from six water bodies in three ecological zones of Nigeria.

2. MATERIALS AND METHODS

2.1 Study Areas

The study areas include six (6) lakes across three ecological zones of Nigeria. These include Asejire (07°2N, 04°7'E) and Oyan (7°15'N, 3°16'E) Lakes from the Southwestern Nigeria (Tropical rain forest); Kanji (10°22'N, 4°33'E) and Jebba (9°8'N, 4°47'E) Lakes from the Northcentral of Nigeria; (Guinea Savannah) and Lake Geriyo (9°18'N, 12°25'E) and Dadin-Kowa (10°18'N, 11°32'E) lakes from the Northeastern Nigeria (Sudan Savannah) as shown in Fig. 1.

2.1.1 Characteristics of the study locations

Asejire Lake: Asejire Lake is a man-made lake that was constructed over River Oshun in 1972 and lies on latitude 07° 2'N and longitude 04° 07'E. It is located about 30 km east of Ibadan, Oyo State, Nigeria. The lake is Y-shaped with two unequal arms of the Y. Catchment area above the dam is 7,800 km² and the impounded area is 2,342 hectares [18]. The lake has a gross storage capacity of 7,403 million litres of water with an elevation of 137 m. It has a relative humidity of 73.4 - 79.1, transparency range between 0.7 - 1.72 m, surface water temperature of 24 - 31.5°C, dissolved oxygen 5.1 - 8.9 mgL⁻¹ and pH 6.2 - 8.5 [18].

Oyan Lake: This is also a man-made lake constructed on the Oyan River in 1983 with an estimated average annual flow of about 1,770

million. It lies on latitude 07° 15'N and longitude 03°16'E. It covers 4,000 hectares and has a catchment area of 9,000 km². It has an average length of 1044m, height of 30.4m with an elevation of 150m above the sea level. Average annual temperature and rainfall are 24.3°C and 102.6 mm respectively with a total capacity of about 270 million [18].

Lake Geriyo: It is a floodplain lake, located on the outskirts of Jimeta metropolis, Adamawa in North-western Nigeria. It lies between latitude 09° 18'N and longitude 12° 25'E. It is a shallow water body with a mean depth of about 2 meters and the mean annual rainfall is between 900 to 1100mm with the rainy season ranging from 150 – 160 days, usually from May to October. Temperature ranges from 20°C in December to January and intense heat with temperatures of 30°C to 42°C from March to April [19]. It experiences some influx of water from floods during the rainy season and overflows from river Benue which serves as a major water source to the lake.

Dandin-kowa Lake: A man-made lake that is located 5km North of Dadin Kowa village (about 37km from Gombe town, along Gombe-Biu road)

in Yamaltu Deba Local Government Area of Gombe State. The area lies within latitude 10°18'N and longitude 11°32'E of the equator. The lake has a water capacity of 800 million cubes and a surface area of 300 kilometers square [20].

Kainji Lake: This is a reservoir on the Niger River, formed by the Kainji Dam. It lies on the latitude 10°22'N and longitude 04°32'Eof the equator. The Kainji Lake basin is one of the most important inland basins in Nigeria, it is the home of the first and the largest hydro-electricity station in the country, and the woodland vegetation of the basin is the home of the first National Parks in Nigeria [21]. According to Ikusemoran and Adesina [22], the impoundment of Kainji Lake on River Niger has converted the river into a lake ecosystem and has also changed the land cover around the formed lake.

Jebba Lake: The lake lies between longitude 04°30'to 04°50'E and latitude 09°55'N. It has a drainage basin extending from Kainji Reservoir to the Jebba area (approximately 100 km). The six major rivers that empty into the lake are Oli, Wuruma, Moshi, Awuru on the western side and Kontangora and Eku on the Eastern part [23].

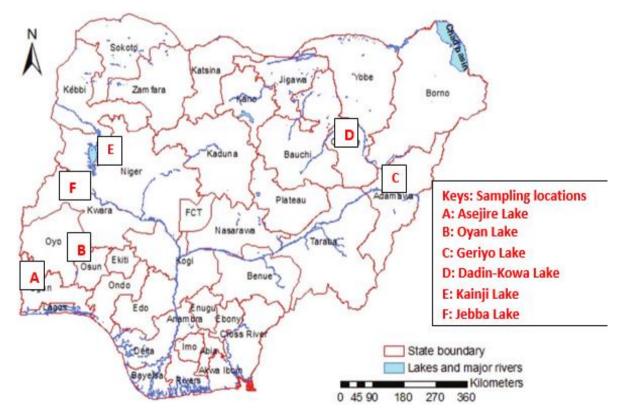


Fig. 1. Map of Nigeria the study locations

2.2 Collection of Sample

Fish samples were collected from the catches of the fishermen at landing sites in each of the study areas. Freshly collected fish samples were transported to the laboratory. Taxonomical identification of the specimens was done using the field guide to Nigerian freshwater fish by Olaosebikan and Raji [24] and Freshwater Fishes of Nigeria by Idodo-Umeh [25]. A total of three hundred and forty-seven (347) individuals of *Oreochromis niloticus* were sampled (Asejire Lake = 62; Oyan Lake = 56; Kainji Lake = 65; Jebba Lake = 56; Geriyo Lake = 55; and Dadin-Kowa = 53) between October 2019 and September 2020.

2.3 Morphometric and meristic Characteristics

Twenty-nine (29) morphological measurements were made on each specimen. Morphometric characters were taken using an absolute digital caliper (Tresna Instruments, 0-150mm range) and all measurements were determined to the nearest millimetre. Measurements were made with the samples facing the left hand side. Body weight was measured using an Ohaun digital weighing balance (Mettler Instrument). The morphometric characters measured include the Total Length (TL), Standard Length (SL), Body Depth (BD), Head Length (HL), Snout Length (SnL), Eye diameter (ED) (Left And Right), Dorsal Fin Length (DFL), Anal Fin Length (AFL), Pelvic Fin Length (PvFL) (Left And Right), Pectoral Fin Length (PFL) (Left And Right), Pre orbital Length (PrOL), Caudal Peduncle Length (CPL), Caudal Peduncle Depth (CPD), Pre dorsal Length (PDL), Pre Anal Length (PAL), Lower Lip Width (LLW), Lower Jaw Width (LJW), Pelvic Distance (PD), Cheek Distance (CD), Lower Lip Length (LLL), Upper Lip Length (ULL), Pelvic Spine Length (PSL) (Left And Right), Last Dorsal Spine (LDS), Third Anal Spine (TAS).

Eight (8) meristic characteristics that were made include Dorsal spine (DS), Dorsal ray (DR), Anal spine (AP), Anal ray (AR), Lower lateral-line scale (LLLS), Upper lateral line scale (ULLS), Left gill raker (Left GR) and Right gill raker (RG).

2.4 Statistical Analysis

All data were normalized by size adjustment before being subjected to statistical analysis. The standardized data were analyzed by univariate and multivariate methods using the Statistical Package for the Social Sciences (SPSS). Differences among sampled populations were tested by one-way analysis of variance (ANOVA). A multivariate test of discriminant function analysis was performed to identify characters that were important in distinguishing the population groups. Softwear and model.

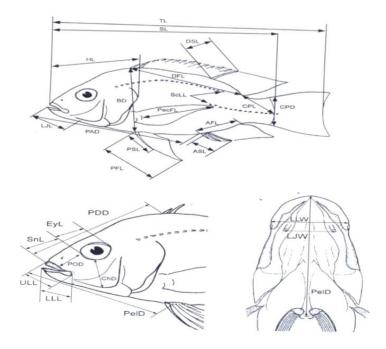


Fig. 2. Map showing the morphometrics characteristics measured Source: Adedeji et al. (2019)

3. RESULTS

The results of the univariate analysis of the morphometric and meristic characteristics are presented in Table I. The results revealed that O. niloticus from Asejire Lake had the highest mean total weight of 255.01±125.29g, followed by 111.57±50.90g and 100.43±42.55g from Oyan Lake and Jebba Lake, respectively, while the lowest mean total weight was observed from Kainji Lake (48.23±39.58) (Table 1). Likewise, the highest mean total length (233.03±53.17cm) and standard length (187.40±43.95cm) were observed from Asejire Lake, followed by Ovan Lake with mean total length and standard length 111.57±50.90cm and 136.50±22.24cm. of respectively, while samples from Kainii Lake had the lowest mean total length (130.22±35.38cm) standard length and (130.22±35.38cm). The body depth of O. niloticus from Asejire, Oyan, Kainji, Jebba, Geriyo, and Dadin-Kowa Lakes was 75.10±14.54 cm, 58.58±9.58cm, 42.96±12.34 cm, 55.74±8.57 cm. 53.46±2.67cm, and 51.51±9.70cm, while the head lengths were 62.03±13.66cm, 46.13±6.99 cm, 36.18±9.96cm, 45.26±6.0 7cm, 40.74±2.94 cm, and 39.10±7.41cm, respectively.

The results revealed that virtually all morphometric characteristics of O. niloticus from Asejire Lake were significantly higher and different (P=.05) from those of other lakes, which simply indicates the heterogeneity of the population, while those of O. niloticus from Geriyo Lake were not significantly different (P=.05) from those of Dadim-Kowa Lake, which indicated the homogeneity of the two populations.

The results from the univariate analysis also showed that all meristcs characters observed across the studied lakes were not significantly different (P=.05) except the gill raker (both left and right) of *O. niloticus* from Geriyo Lake, which is significantly different from that of Asejire, Oyan, Kainji and Jebba Lakes but not significantly different from that of Dadin-Kowa Lake (Table 1). The result further revealed that there is no significant difference (P=.05) in the gill raker counts of *O. niloticus* from Asejire, Oyan, Kainji, Jebba and Dadin-Kowa Lakes.

In the study areas, the standardized canonical discriminant function coefficient for O. niloticus three morphometric revealed that and four meristic characters were the most discriminating among the populations. The three discriminating morphometric characters were body weight, anal fin length, and caudal peduncle length, while the four discriminating meristic characters were the upper lateral line scale, lower lateral line scale, left gill raker, and right gill rakers (as shown in Table 2). By referring to the standardized discriminant function coefficient (Table 2), we can conclude that positive coefficients indicate that higher values of the characters contribute to the discrimination between sampled species from different sites. Conversely, negative coefficients suggest that lower values of the characters are responsible for discriminating between the sampled species from different sites. Additionally, the magnitude of the coefficient represents the strength of the contribution of the characters in the species discrimination. Larger magnitude coefficients have a greater impact on group discrimination.

standardized The discriminant function coefficient (Table 2) indicates that the right gill raker (0.999) has a higher value and makes a stronaer contribution to differentiating the sampled O. niloticus from various sites, while the body weight (-0.079) has a lower value and a weaker contribution. This is reflected in the discriminant plot (Fig. 3), where sites with higher gill raker values appear on the right (positive) side of function 1, and those with lower raker values appear on the left aill (negative) side. Similarly, the plot also shows that sites with lower body weight values fall on the left side of function 1, while sites with higher body weight values fall on the right side. The standardized discriminant function coefficient indicates that body weight has a weaker contribution to the species discrimination. The canonical discriminant plot (Fig. 3) also shows that the O. niloticus populations from Geriyo Lake and Dadin-Kowa Lake form a cluster, and similarly, the populations from Kainji Lake and Jebba Lake form another cluster on the plot.

	Asejire	Oyan	Kainji	Jebba	Geriyo	Dadin-Kowa
Characters	Mean±SD	Mean±SD	Mean±SD	Mean±SD	Mean±SD	Mean±SD
TW(g)	255.01±125.29ª	111.57±50.90 ^b	48.23±39.58 °	100.43±42.55 °	66.84±13.62 ^d	73.02±44.96 d
TL(cm)	233.03±53.17 ^a	171.81±25.63 ^b	130.22±35.38 d	168.34±23.90 ^b	150.16±10.67 °	150.59±27.03 °
SL(cm)	187.40±43.95 ^a	136.50±22.24 ^b	102.91±27.84 ^d	134.45±19.37 ^b	118.55±8.77 °	119.84±22.76℃
BD(cm)	75.10±14.54 ª	58.58±9.58 ^b	42.96±12.34 ^e	55.74±8.57 bc	53.46±2.67 ^{cd}	51.51±9.70 ^d
HL(cm)	62.03±13.66 ª	46.13±6.99 ^b	36.18±9.96 ^d	45.26±6.07 ^b	40.74±2.94 °	39.10±7.41 °
SnL(cm)	20.67±4.82 ª	14.85±2.37 ^b	12.46±5.02 °	14.37±2.41 ^b	12.54±1.49 °	12.34±2.86 °
EDL(cm)	12.64±1.87 ª	9.71±1.28 ^b	9.11±1.36 ^b	10.22±0.99 ^b	9.41±0.64 ^b	9.12±1.12 ^b
EDR(cm)	12.71±1.84 ª	9.88±1.50 ^b	9.13±1.39 ^b	10.30±0.75 ^b	9.52±0.69 ^b	9.38±0.98 ^b
DFL(cm)	115.54±26.27 ª	83.87±13.61 ^b	61.22±18.24 °	78.14±20.20 °	72.29±4.97 ^d	71.46±18.83 d
AFL(cm)	38.19±9.78 ^a	25.02±7.63 ^b	19.38±5.45 ^d	26.88±4.02 ^b	23.28±2.27 °	22.93±4.77 °
PFLL(cm)	48.30±9.18 ^a	37.28±5.67 °	30.98±8.57 ^d	41.34±6.72 ^b	36.53±2.95 °	31.04±7.30 ^d
PFLR(cm)	49.55±8.84 ^a	37.24±5.91 °	31.35±8.22 d	41.30±6.55 ^b	35.82±2.65 °	30.80±7.27 ^d
PcFL(cm)	69.67±16.14 ª	50.41±9.38 ^b	37.12±12.31 ^f	49.98±9.90 °	45.54±3.49 ^d	42.57±8.85 ^e
POL(cm)	11.77±3.01 ª	7.86±1.42 ^{bc}	6.11±2.05 °	8.07±1.44 ^b	7.11±0.81 ^{bc}	6.80±1.78 °
CPL(cm)	24.46±6.31 ª	17.38±3.70 ^b	12.18±3.66 d	15.87±2.21 °	15.85±1.74 °	15.33±3.43 °
PDL(cm)	64.65±14.53 ^a	48.41±7.28 ^b	36.49±10.52 ^d	47.68±5.76 ^b	42.01±3.41 °	42.71±8.15 °
PAL(cm)	135.04±30.57 ^a	101.42±16.53 ^b	74.73±19.56 d	102.15±12.99 ^b	87.52±7.13 °	88.68±16.97 °
LLW(cm)	18.14±5.10 ª	13.41±2.80 ^b	9.26±3.44 ^d	12.54±2.57 ^{bc}	11.13±1.34 ^{bc}	10.68±2.72 ^{cd}
LJW (cm)	15.47±4.30 ª	11.63±2.43 ^b	7.97±2.83 ^d	10.66±1.93 ^{bc}	9.14±0.88 ^{cd}	9.00±2.39 ^{cd}
PD(cm)	80.21±16.43 ª	59.17±8.58 ^b	43.28±14.69 °	59.78±7.76 ^b	53.36±3.27 °	50.01±9.52 d
CD(cm)	19.62±5.12 ª	14.07±2.53 ^b	10.37±3.62 °	13.65±2.16 ^b	12.37±1.15 bc	12.00±3.41 bc
LLL(cm)	12.74±3.67 ^a	9.23±1.51 ^b	7.12±2.06 °	8.87±1.49 ^{bc}	8.11±0.96 ^{bc}	8.26±1.62 bc
ULL(cm)	14.63±4.16 ª	11.06±1.90 ^b	8.31±2.54 °	10.58±2.30 ^b	9.62±1.13 ^{bc}	9.43±1.92 bc
CPD(cm)	28.02±6.32 ^a	20.49±3.72 ^b	15.21±4.81 ^d	19.46±2.98 bc	18.58±3.20 bc	17.68±3.70 °
PSLL(cm)	26.22±5.34 ^a	20.97±2.48 ^b	17.55±5.16 °	21.58±2.74 ^b	19.80±1.79 ^b	16.29 ± 2.66 °
PSLR(cm)	26.75±5.26 ^a	20.86±2.59 bc	17.72±5.39 d	21.90±2.60 ^b	19.46±1.43 °	16.44±2.64 ^d
LDS(cm)	27.15±5.43 ª	20.77±2.84 ^b	16.09±5.25 d	22.12±2.67 b	19.41±1.55 ^{bc}	17.44±3.30 ^{cd}
TAS(cm)	28.46±5.38 ^a	21.58±2.60 ^b	16.84±5.64 °	21.17±2.87 ^b	20.87±1.19 ^b	17.55±3.35°

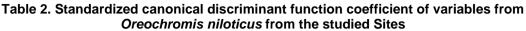
Table 1. Mean values and standard deviation of morphometric and meristic characteristics of Oreochromis niloticus across diverse ecological zones in Nigeria

	Asejire	Oyan	Kainji	Jebba	Geriyo	Dadin-Kowa
Characters	Mean±SD	Mean±SD	Mean±SD	Mean±SD	Mean±SD	Mean±SD
Meristic Characters						
DS	17.18±0.39	17.18±0.39	16.95±0.51	16.80±0.41	17.06±0.24	17.10±0.31
DR	12.06±0.24	12.12±0.60	12.25±0.64	12.35±0.49	12.24±0.56	12.70±0.47
AS	3.00±0.00	3.00±0.00	3.00±0.00	3.00±0.00	3.00±0.00	3.00±0.00
AR	9.29±0.69	9.18±0.39	8.95±0.22	8.95±0.39	9.06±0.43	9.00±0.00
ULLS	22.06±0.75	21.41±0.71	21.45±0.60	22.80±0.95	22.12±0.60	22.10±0.64
LLLS	14.53±0.80	14.35±0.70	13.70±0.47	13.95±0.76	14.47±0.94	14.00±0.00
GRL	22.59±0.62ª	22.47±0.62 ^a	22.70±0.47 ^a	22.55±0.51 ^a	20.59±1.28 ^b	21.45±0.51 ^{ab}
GRR	22.71±0.47ª	22.53±0.51ª	22.60±0.50 ^a	22.50±0.51ª	20.94±0.97 ^b	21.45±0.51 ^{ab}

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*SD – Standard Deviation

			Functions		
	1	2	3	4	5
BW	-0.079	-2.956	-0.953	0.346	0.282
AFL	0.390	1.486	0.110	1.464	0.649
CPL	-0.411	1.409	1.514	-1.518	-1.270
ULLS	0.079	-0.039	0.408	0.558	0.456
LLLS	0.124	0.319	-0.639	0.169	-0.269
GR_left	0.002	0.243	-0.206	-0.749	0.646
GR_right	0.990	-0.124	0.077	-0.018	-0.012



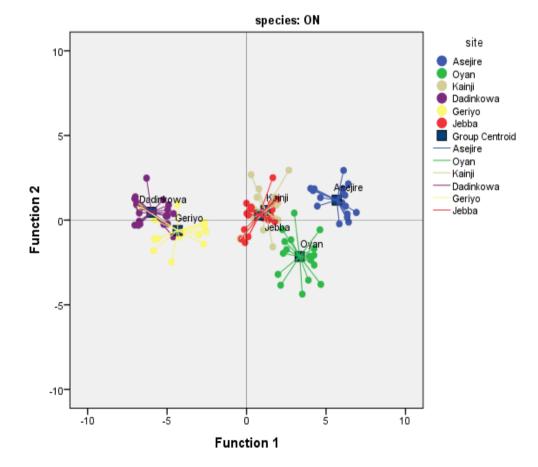


Fig. 3. Canonical discriminant plot for Oreochromis niloticus from the studied sites

4. DISCUSSION

Morphological characters including morphometric, meristic and truss network system have been widely used to delimit the various populations of fish stock from different aquatic environments [26]. The observed variations in the morphometric and meristic characteristics of *O. niloticus* from the present study are similar to the reports of Adedeji et al. [14] that observed anal fin length and right gill rakers among other characters as discriminating characters in *Coptodon zilli* from some major water bodies in Nigeria. This present study also showed some level of similarities with the work of Akinrotimi et al [15] who observed *Sarotherodon melanotheron* from three different Creeks in River State to be phenotypically separable population based on the variations in their body depth and caudal peduncle length.

The results from this present study also corroborate with the reports of Ezeafulukwe et al [13] who reported significant variations in the

body depth and caudal peduncle width in Hemichromis fasciatus from two aquatic environments (rivers and ponds) in Imo state Nigeria and the work of Oyewunmi et al [11] also revealed eye diameters, caudal peduncle depth and spinous dorsal fin ray as discriminating characters in Sarotherodon galilaeus from three man-made lakes in Nigeria. The reports of Kuton and Adeniyi [10] revealed body depth, caudal peduncle depth, and the number of gill rakers as discriminating characters in Sarotherodon melanotheron from two lagoons, Badagry and Lagos lagoon. However, the present study is not in total submission to the work of Ben et al. [16] who observed caudal peduncle depth as a nondiscriminating character in the racial study of Boops boops from four marine stations along the Tunisia coast. There were no significant variations observed in the fin ravs of O. niloticus from the six study areas, as they remain fairly constant which agrees with the theory of Reed [27] that fin rays of cichlids do not vary much. Moreover, fin ray counts and vertebrae numbers were reported to have been established early in larval development and are influenced by temperature Taning [28]. Consequently, the lesser variations in the meristic characters across the studied areas may suggest that the development of the larvae experienced less distinct environmental conditions even though they are from different ecological zones.

The morphometric parameters observed in O. niloticus from Asejire and Oyan lakes were significantly higher than those of Geriyo and Dadin-Kowa lakes. This difference could be attributed to the availability of food and other environmental factors. According to Eyo [29], food availability contributes to high morphological plasticity in fish. Geriyo and Dadin-Kowa are known to be less productive [14,30], which could result in low availability of food. In the present study, significant variations in head-related measurements were also observed between O. niloticus from Asejire Lake and other lakes, confirming previous reports that variations between populations of tilapia species are mostly reflected in the head region [31]. Adedeji et al [14] also observed similar variations in the head measurements of Coptodon zillii from five different water bodies in Nigeria. The variations observed in the morphometric and meristic characters in O. niloticus from the six study areas could be due to environmental factors such as temperature, salinity, geographical isolations, and genetic compositions, as established by different researchers.

There were some level of overlapping of O. niloticus populations observed between the populations of Geriyo and Dadin-Kowa lakes, as well as between the populations of Kainji and Jebba lakes, as shown in the canonical discriminant plot. This overlapping was due to some level of similarity or fewer variations in the studied characters, which may be attributed to the fact that both lakes are located in the same ecological zone (Sudan savannah) of Nigeria and experience the same environmental conditions, such as temperature. Even though Geriyo Lake is a natural lake and Dadin-Kowa is a man-made lake, there was no evidence of connections between the two lakes. Similarly, the overlapping between O. niloticus from Kainji and that of Jebba could simply be attributed to the fact that both lakes are in the same ecological zone, and there was evidence of linkage between the two lakes.

5. CONCLUSION

In summary, the current study has confirmed that differences in size and count of certain body features among populations of a species are important for evaluating the population structure. These features remain reliable tools for identifying different populations. The study identified three size-based features and four count-based features distinguishing as characteristics in O. niloticus from six water bodies in Nigeria. O. niloticus from Asejire Lake had significantly larger size-based features compared to the other locations, while those from Geriyo Lake and Dadin-kowa had the smallest size-based features. The observed differences in the appearance of O. niloticus in the studied areas may be due to factors such as temperature, food availability, geographical isolation, and genetic variation. The current study supports the idea that there is significant variation in the appearance of *O. niloticus* within different populations due to environmental factors and genetic differences.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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