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MORPHOLOGICAL DIFFERENCES AND TROPHIC NICHE BREADTH OF *Sarotherodon galilaeus* AND *Oreochromis niloticus* FROM THE FRESHWATER LAKE GERIYO, NORTH-EASTERN NIGERIA

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ABSTRACT

The relationship between morphological traits and feeding ecology of the only two tilapiine cichlids (*Sarotherodon galilaeus* and *Oreochromis niloticus*) in Lake Geriyo, northeastern Nigeria, was examined. Stomach contents of 504 individuals were examined and analyzed to relate morphological differences of each species to its dietary preferences. Eleven ecological relevant morphological variables, including total length, standard length, head length, body depth, eye diameter, pectoral spine length, pelvic spine length, dorsal fin ray count, dorsal spine count and anal fin ray count, were also measured and subjected to Principal coordinate analysis (PCoA) to relate morphological differences of each species to its dietary preferences. The PCoA (using Euclidean distance) revealed a large morphological distance between species indicating adaptation for different spatial and vertical distributions within the lake. Furthermore, the correlation of these morphological differences with particular diet categories suggests a potential for specialized trophic tendencies, however, the high occurrence of two major food types (macrophytes and plankton) in stomach contents of both species indicate generalist trophic tendencies. While a high trophic overlap index (0.98) was recorded for both species, the trophic niche breadth was higher for *S. galilaeus* (4.18±0.32), compared to *O. niloticus* (3.33±0.24). Despite the large morphological differences of both tilapias, the high trophic overlaps indicate limited food options within Lake Geriyo. In addition, the successful coexistence of the tilapias in the face of limited food resources indicates suitable partitioning of food resources in the lake.

How to Cite

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INTRODUCTION

The fundamental niche of a species can be defined as the set of abiotic environmental conditions within which a species can survive and maintain viable populations (Degerman et al., 2007; Holomuzki et al., 2010; Ibor et al., 2017). Since the survival of organisms is a function of their ability to adapt to each or a combination of these interacting factors, the prevailing features of a habitat, including their environmental conditions, will determine phenotypic attributes of organisms by filtering specific traits (Hart, 1993; Silva et al., 2014; Welsh, 2013). This environmental filtering theory has been demonstrated by relating morphology of a species to its niche preference and habitat use in a specified environment (Douglas and Matthews, 1992; Wainwright and Reilly, 1994). Thus, every habitat presents a set of restrictions that ensure survival of individuals with the best adaptive morphological characteristics (Motta et al., 1995b). The selected characteristics often manifest in form of feeding constraints, different reproductive strategies and competition for space or complex interactions with other species (Cunico and Agostinho, 2006; Mérona and Rankin-de- Mérona, 2004; Mindel et al., 2016).

Ecological constraints due to varied morphology of species are mostly centered around food and space because they constitute key ecological resources shared between species in every habitat (Mérona and Rankin-de-Mérona, 2004). As a result, particular morphological features are linked to trophic preference or habitat patch being harnessed by the species (Ehlinger and Wilson, 1988; Wainwright, 1988). Several theories have offered strategies for resource control among co-existing populations (Adite and Winemiller, 1997). The *niche filtering hypothesis*, for instance, seeks to address the number of species adapted to harness limited resources available to a community (Tonn et al., 1990; Zobel, 1997), while the *competitive exclusion principle* implies that two species competing for a critical resource in an environment can successfully coexist if the shared niche is effectively partitioned (Adite and Winemiller, 1997). Trait-based studies have been used to understand how resources are partitioned between species in a community and have also been used to simplify ecological models in species-rich communities (Corrêa et al., 2011; Yang et al., 2015).

The use of morphological traits to predict ecological relationships between body form and niche function have been explored and documented for various vertebrate groups, including some freshwater fish species (Davis et al., 2012; Watson and Balon, 1984; Ibor et al., 2017; Carroll et al., 2004; Hjelm et al., 2003). This is because morphological features and patterns of development have been shown to be highly conserved within some clades (Finnegan, 2017). Many studies have focused on the morphological characteristics of structures related to food acquisition since they allow inferring in diet preferences of species (Ibañez et al., 2007; Lima-Junior

and Goitein, 2003) (Cassemiro et al., 2008; Kramer and Bryant, 1995). For example, gape size and number of gill-rakers are suggestive of type and size of prey consumed by a species (Boubee and Ward, 1997; Salman, 2005). The use of traits like body depth and pectoral fin size to predict whether a fish inhabits areas of strong water current or open water zones have also been documented (Lauder and Madden, 2007). All approaches demonstrate that niche differentiation among species is driven in part by morphological divergence, where traits determine what trophic options could be exploited and which habitat terrains could be explored or accessed (Ford et al., 2016; Tamburri and Barry, 1999). As such, given that food resources and habitat space are major lines driving niche partition between aquatic vertebrates (Ross, 1986; Mérona and Rankin-de-Mérona, 2004), it is logical to think that different species can either exploit different resources or share the same food resource depending on its availability (Novakowski et al., 2008, Pouilly et al., 2006).

Some reports on the trophic ecology of tilapiine populations in Nigerian freshwater systems include the food and feeding habits of several species in Lake Eleyele, South-West Nigeria (Ayoade and Ikulala, 2007), and the growth and condition factor of *Oreochromis niloticus* and *Sarotherodon galilaeus* in Lake Geriyo (Adedeji et al., 2016). Lake Geriyo represents a strong break along the course of the River Benue, and is one of the most anthropogenically impacted impoundments north of the River Benue, with intermittent nutrient input and gradual changes in habitat morphology (Ezekiel et al., 2015). Although the fishery of Lake Geriyo is a strategic economic and ecological freshwater resource, *Clarias* and *Tilapia* are the most abundant commercial genera (Ekundayo et al., 2014), structural and functional aspects of the fish communities in this lake are still unknown. It is expected that information on the life history and trophic ecology of representative species will reflect the effect of the perturbed environment. Tilapia are model species for ecological studies and their welldescribed morphology and tendency for adaptive radiation could give great insight into the partitioning of resources within a fresh water lake (Piet et al., 1994; Beveridge and McAndrew 2012; Njiru et al., 2007). In addition, the potential of tilapiine cichlids to exhibit guilds tendencies (tending to exploit the same kinds of resources in comparable ways) has been documented for certain environments (Zengeya et al., 2015). The ease of using of guild species for niche overlap studies has been recommended second because niche overlaps are easier studied between guilds, i.e. species that use resources in similar ways (Bonato et al., 2012). Although several studies have investigated the relationship between the morphological attributes and diet preferences of tropical African species (Offem et al., 2009; Adite and Winemiller, 1997; Faye et al., 2012; Hugueny and Pouilly, 1999), findings are not often discussed in the context of ecological or conservation theories. This paper reports

the use of a morphometric trait-based approach to gain insight into the trophic strategies of tilapiine populations in a freshwater lake north-west of Nigeria, West Africa. The objective of this study is to explore the relationship between the morphological traits and diet ecology of the only two tilapiine cichlids within Geriyo freshwater lake and discuss the findings in the light of the *niche filtering hypothesis* and *the competitive exclusion principle*.

MATERIAL AND METHODS

Study site

Lake Geriyo is located on the outskirts of the Jimeta metropolis, in the state of Adamawa, in the Northeast Nigeria (12° 25'E -12° 26'E, 9° 17'N - 9° 19'N, Fig. 1). It is a shallow water body with a mean depth of 2 meters. This area receives rainfall with a range of between 900 – 1100 mm, with the rainy season spanning 150 -160 days, usually between May and October. The average annual temperature is 26.8°C; climatic conditions vary from 20°C, with cold and dusty winds in December and January, to intense heat between March and April with temperatures ranging from 30°C to 42°C. It experiences an influx of water during the rainy season from the River Benue, which serves as a major water source to the lake. Aquatic vegetation consists of floating weeds, such as water hyacinth, typha grass, water lily and wild guinea corn, which drift around the lake surface in response to the direction of prevailing winds (NIFFR, 2002).

Sample collection

Two tilapiine cichlid species (Fig. 2a and 2b) from Lake Geriyo, *Oreochromis niloticus* (n=276) and *Sarotherodon galilaeus* (n=228), were sampled twice a month across seasons over a six-month period (January-June 2015), between 09-12 h local time, using gill net (50- 55 mm mesh size). The period between January and April represents the dry season, while between May and June represents the rainy season. Specimens collected were preserved in an ice chest during transport to the laboratory.

Sample identification and morphometric measures

Fish samples were identified following Olaosebikan and Raji (2013). A total of eleven ecologically relevant morphological attributes, including seven morphometric and four meristic characters, were measured in fish samples (adapted from Adite and Winemiller 1997). Total length (TL) was measured from the tip of the snout (mouth closed) to the extended dorsal tip of the caudal fin; standard length (SL) was measured from the tip of the snout to the mid-lateral tip of the caudal peduncle; head length (HL) was measured from the front of the snout to the back of the operculum; body depth (BD) was measured as the vertical distance from the dorsal margin of the body to the ventral margin of the body at the base of the pelvic fin where it attaches to the body; fins or fin bases are not included in the measurement; maximum eye diameter (ED) was measured as the horizontal distance between both lateral eye margins; pectoral spine length (PecSL)

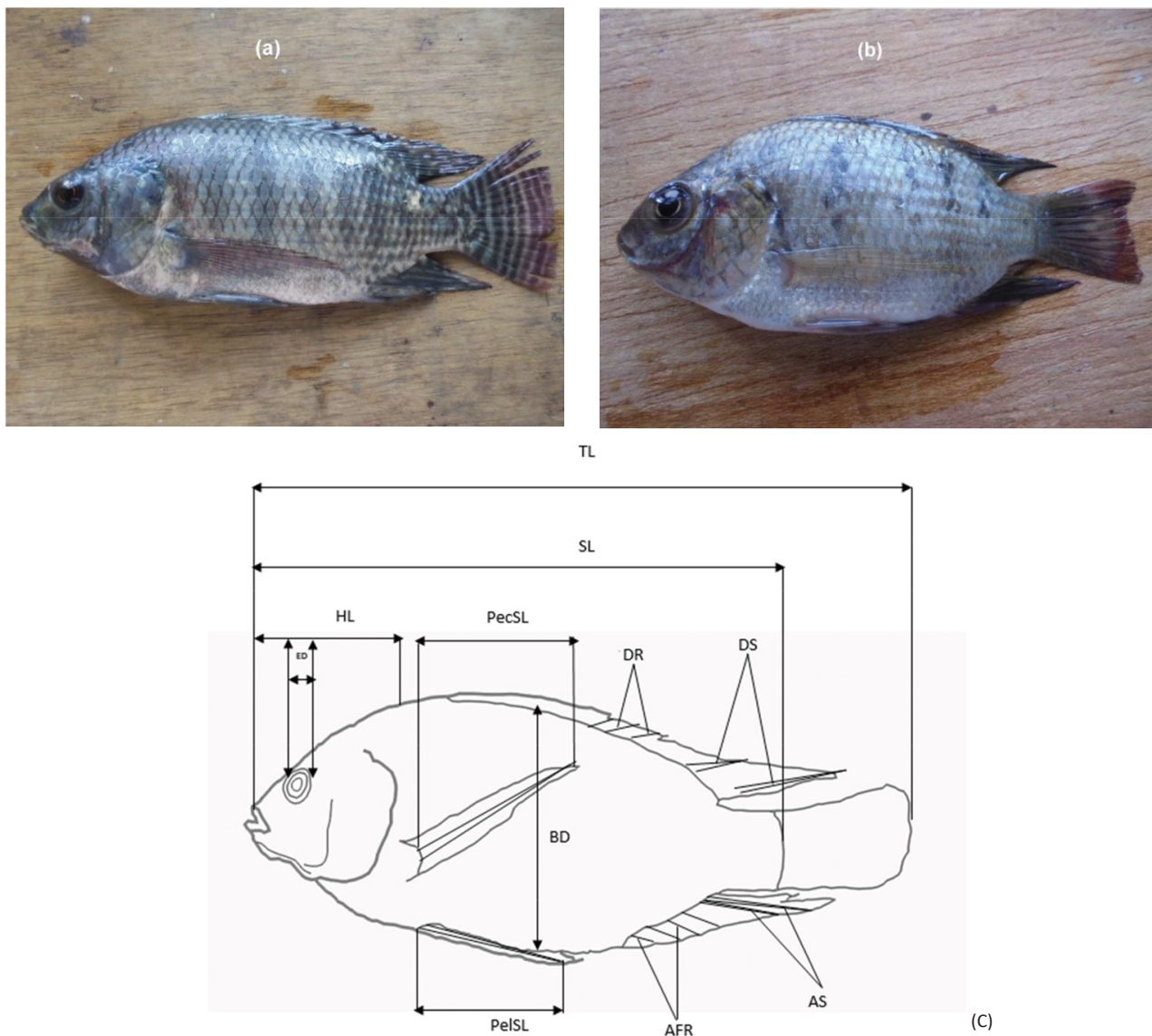**Fig 1.** Map of Lake Geriyo, Adamawa state, Nigeria

Fig 2. Picture of (a) *Oreochromis niloticus* (b) *Sarotherodon galilaeus* (c) Schematic body plan of tilapia showing morphometric measurements and meristic features: where HL (Head length), PecSL (Pectoral spine length), PelSL (Pelvic Spine length), ED (Eye diameter), BD (Body depth), AFR (Anal Fin Ray), AS (Anal Spine), DS (Dorsal spine), DR (Dorsal ray), SL (Standard length), TL (Total length)

was measured from its insertion on the pectoral fin to the tip of its spine; pelvic spine length (PelSL) was measured from its insertion on the pelvic fin to the tip of its spine. Meristic counts included dorsal fin-ray count (DFRC), dorsal spine count (DSC), anal fin ray count (AFRC) and anal spine count (ASC) (Fig. 2c). Morphometric features were measured using Vernier calipers to the nearest 0.1 mm, while meristic characters were counted.

Stomach fullness analysis

The gut was opened to observe the gut fullness, which was categorized as 0 (empty), 1 (¼ full), 2 (½ full), 3 (¾ full) or 4 (full) based on Begum et al. (2008). The number of stomachs containing each food item was expressed as a percentage of all non-empty stomachs, following

the frequency of occurrence method (BaŞusta, 2012). This method was chosen because it is quick and requires minimal apparatus (BaŞusta, 2012).

Stomach content analysis

Specimens were cut open, and stomachs were removed from specimens and were immersed in 4% formalin. Each stomach was slit open and the contents emptied into a petri dish. Contents were first observed by eye and stomach contents were thereafter placed on slides with the aid of a dropping pipette for observation under a light microscope. After the stomachs were examined for gut-fullness, the contents were identified and analyzed using the numerical and frequency of occurrence methods (Bagenal and Tesch, 1978). The numerical method is the

individual measure of each stomach, while the frequency of occurrence is a collective measure that includes all the analyzed specimens of each species.

The numerical method involves counting the number of

$$N(\%) = \frac{Total\ number\ of\ a\ particular\ food\ item}{Total\ number\ of\ all\ food\ items} \times 100$$

each food item-type present in the stomach of a fish. The number can then be expressed as a percentage of the total number of food items found in the stomach N (%).

The frequency of occurrence method involves counting the number of times that each food item occurs (one count per stomach) and expressing it as a percentage of

$$F(\%) = \frac{Total\ number\ of\ stomachs\ wiht\ a\ particular\ food\ item}{Total\ number\ of\ stomachs\ with\ food} \times 100$$

the total number of stomachs containing food, excluding the empty stomachs.

Percentage of occurrence of a food item F (%):

Trophic niche analysis

To facilitate comparisons between species, prey and diet items were identified, but summarized into basic trophic categories: detritus, macrophytes, plankton, insects and unidentified matter according to Winemiller (1992).

Trophic niche breadth

Based on the food categories identified from the study

$$B = \frac{1}{\sum p_i^2} \qquad (1)$$

of stomach contents, trophic niche breadth (Levins, 1968) was used to ascertain the trophic niche difference between the two tilapiine species in Lake Geriyo, and was calculated from the formula

Where B is the trophic niche breadth and p_i is the numeric proportion of the food item i in the diet. The B ranges from 1, when only one resource is used, to n, when all resources are used equally by the consumer.

According to Krebs (1989), the maximum value for diet breadth is obtained when all resources are equally available and the consumer shows no discrimination. Based on Grossman (1986), trophic niche breadth was considered low (0 - 0.39), intermediate (0.4 - 0.6) or high (0.61 - 1).

The standardized niche breadth (B_a) was also calculated following Hurlbert (1978):

$$B_a = (B - 1) / (n - 1) \qquad (2)$$

B_a ranges from 0, when only one resource is used, to 1 when all resources are used equally. The n is the total number of food categories in the diet.

Mean trophic niche breadth for each month of the sampling period was computed from semimonthly samples. Difference in monthly mean niche breadth between species were tested using the Student's t-tests (p<0.05).

Trophic overlap index

In contrast to niche breadth, the parameter niche overlap measures the degree to which two different species overlap in their use of a particular resource. This measure helps to understand how different species partition their

$$O_{jk} = \frac{\sum p_{ij}p_{ik}}{\sqrt{\sum p_{ij}^2 p_{ik}^2}} \qquad (3)$$

resources within the community. If species overlap in niches to a great extent, they may influence each other's population growth through interspecific competition. As the case for niche breadth, niche overlap can be measured in a variety of ways (Krebs, 1989). The niche overlap index was calculated according to Pianka (1986) which is calculated as:

where O_{jk} is Pianka's measure of overlap between species j and species k, p_{ij} is the proportion that resource i is used by species j of the total resources, and p_{ik} is the proportion that resource i is of the total resources used by species k. This measure ranges from 0 (no resources used in common) to 1 (complete overlap). Diet overlap between species was considered as low (0 - 0.39), intermediate (0.4 - 0.6) or high (0.61 - 1) (modified from Grossman, 1986).

Statistical analysis

The box plot integrated with size frequency histogram was used to describe the distribution of morphometric features within each population. Morphometric variables situated on the head were expressed as a proportion of head length, while standard length was expressed as a proportion of the total length; other body variables were expressed as a proportion of standard length (Gatz, 1979, Önsoy et al., 2011). While the histogram represents the skewed distribution of a particular morphometric variable in the population, relatively smaller-width box plot indicates that a morphometric feature is conserved, i.e. showed limited variation in morphology within the population (Finnegan, 2017, Cole and Shapiro, 1990, Hume, 2013). Due to the fact that meristic features are largely conserved and as such will be poorly depicted on histograms and box plots, difference in meristic counts between the two populations were analyzed and described using Students t-test values.

All statistical procedures were performed on Z- scores of morphological data sets. Principal coordinate Analysis (PCoA) was performed on diet types and morphological datasets of each species (Zuur et al., 2007) to elucidate the correlation between eco-morphological variables and species, while lessening the influence of variables that contribute relatively little to their overall relationship (Jeffers, 1978). Principal coordinate Analysis (otherwise called multidimensional scaling in SPSS) was run in SPSS environment. The PROXSCAL was used for specifying,

Euclidean distances for data, Torgerson's Initial configuration and setting Maximum iterations to 100.

From the output, if the combination of the first two components account for up to 50% of the total variance, PCoA biplots will be limited to the first two components, while the remaining PCs will be excluded from its interpretation (Field, 2009). Coefficients of variables within each principal component were considered significant using Stevens' table of critical values (Stevens, 2002). Histogram and box plot depictions of morphometric data were plotted using iNZight ® version 3.02 (Freeware). Bar charts and error bars were plotted using Originlab version 9.0 (OriginLab, USA) while Student's t-test and multivariate analysis were performed in Statistica® version 12 (StatSoft, Inc., USA).

of the *O. niloticus* population was normally distributed, with a larger percentage of individuals having longer body lengths compared to *S. galilaeus*, which showed a negative skew towards individuals of shorter length (Fig. 3a). The *O. niloticus* population shows a more conserved range of SL compared to *S. galilaeus* as indicated by its smaller interquartile range. The wider interquartile range of *S. galilaeus* depicts a wider variability in size lengths of individuals with a skew for smaller sized individuals. Similarly, BD (expressed as a proportion of standard length) of the *O. niloticus* population was normally distributed in the population, with a larger percentage of the population having BD values of 0.4; on the other hand, BD in the *S. galilaeus* populations was positively skewed, indicating that a larger percentage of the population

Table 1. Mean morphometric and meristic variables for *O. niloticus* and *S. galilaeus* from Lake Geriyo

	O. niloticus		S. galilaeus	
	Mean	SD	Mean	SD
TL	15.22	1.63	16.21	1.39
SL	11.80	1.32	12.45	1.22
BD	4.82	0.52	5.61	0.76
HL	4.09	0.46	4.37	0.46
DFRC	12.56	0.58	12.88	0.33
DSC	17.04	0.20	16.02	0.25
ED	0.98	0.07	0.99	0.06
PelSL	1.92	0.29	2.34	2.41
PecSL	4.33	0.46	4.99	0.53
AFRC	9.06	0.25	10.90	0.30
ASC	3.00	0.00	3.00	0.00

Where SD= standard deviation

RESULTS

Morphometric analysis

Descriptive analysis of morphometric and meristic variables (Table 1) reveals that *S. galilaeus* was larger sized than *O. niloticus* in most morphometric variables (TL, SL, BD, HL, ED, PelSL, PecSL).

From the histogram box plot (Fig. 3), the population of the two species showed different morphological tendencies. Standard length (expressed as a proportion of total length)

tended towards having a larger BD (Fig. 3b). This indicates that *O. niloticus* is more elongated in appearance while *S. galilaeus* is more rounded in appearance.

From Fig. 3c, HL (expressed as a proportion of standard length) of *O. niloticus* was skewed towards a smaller-sized head (<0.34) compared to *S. galilaeus* population which was normally distributed around a larger-sized head (0.34 and 0.36). Although ED was negatively skewed in both populations, *O. niloticus* were distributed over a larger eye-to-body proportion (0.82) compared to *S. galilaeus* (0.76) (Fig. 3d). Similarly, PecSL (expressed as a median
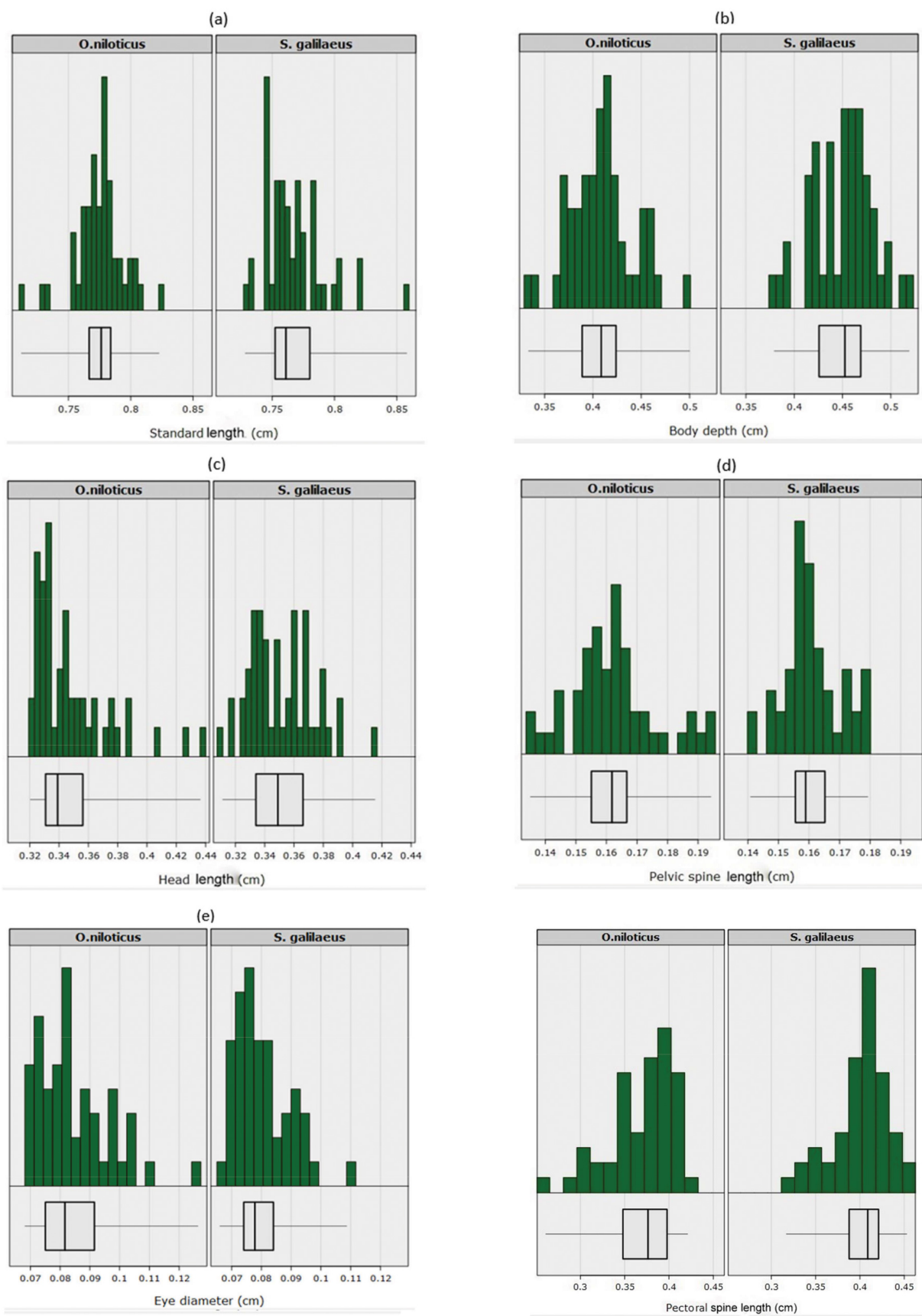
Fig 3. Histogram and box plot of morphometric variables (a) standard length (b) body depth (c) head length (d) pelvic spine length (e) eye diameter (f) pectoral spine length of Sarotherodon galilaeus and Oreochromis niloticus from Lake Geriyo; where box= interquartile range (50% of population), mid-line= median value of the population, left and right whisker= upper and lower quartile, respectively

length for *S. galilaeus* population (0.41) indicated that they had a generally larger pectoral fin length than the *O. niloticus* population (0.38) (Fig. 3e). From Fig. 3f, the pelvic spine length (expressed as a proportion of standard length) was positively skewed in *O. niloticus* population with a median length of 0.164, while the distribution for *S. galilaeus* population was negatively skewed with a median length of 0.158.

Meristic features

Difference in mean meristic count reflected significant differences ($p < 0.05$). A higher anal fin ray count (AFRC) and dorsal fin ray count (DFRC) (10.9±0.43; 12.88±0.05, respectively) was recorded for the *S. galilaeus* population in Lake Geriyo compared to the *O. niloticus* population (9.06±0.34; 12.56±0.08, respectively). However, the *O. niloticus* population had a significantly higher mean dorsal spine count (DSC) (17.04±0.28) compared to the *S. galilaeus* population (16.02±0.35) in Lake Geriyo (see supplementary table for mean values of all morphometric and meristic values for both species).

Diet Analysis

Stomach Content Analysis

Analysis of stomach contents showed that 75% of *S. galilaeus* examined had full stomachs (4/4), while the remaining twenty-five percent were three quarter full (3/4). *O. niloticus* had 37.5% of samples with empty stomachs (0/0), 25% of samples had half full stomachs

Table 2. Numerical contribution (N %) and frequency of occurrence (F %) of food items found in the stomach of *S. galilaeus* and *O. niloticus*

	S. galilaeus		O. niloticus	
	%N	%F	%N	%F
Insects parts	10.29	75	6.61	40
Planktons	28.68	100	30.15	100
Macrophytes (plant materials)	22.30	100	32.72	100
Detritus	6.62	50	4.78	20
Unidentified materials	24.26	100	25.74	100

(2/4), while 12.5% were 1/4, 3/4 and 4/4, respectively. The food particles sampled from the guts of the two populations were identified and broadly categorized into planktons, insect parts, plant particles/macrophytes, detritus and unidentified particles. Most stomachs of both species were observed to contain mainly plankton and macrophytes. Contrastingly, a higher proportion of

insect parts and detritus were observed in stomachs of S. galilaeus compared to *O. niloticus* (Table 2).

Trophic niche breadth

Although all diet item categories were similar between the two species, *S. galilaeus* (4.18±0.32) had a larger mean niche breadth than *O. niloticus* (3.33±0.24). This indicates that *S. galilaeus* had a greater spread of dietary items than *O. niloticus*. A breakdown of niche breadth according to seasons (Figure 4a) showed that in spite of the smaller niche breadth of *O. niloticus* compared to *S. galilaeus*, niche breadth for both species increased gradually and in parallel from the dry season into the rainy season. The slight increase in niche breadth transiting into the rainy season suggests that the onset of rains may increase the availability of food offering the possibility to the species to access a wider range of trophic options. (Fig. 4a). Analysis
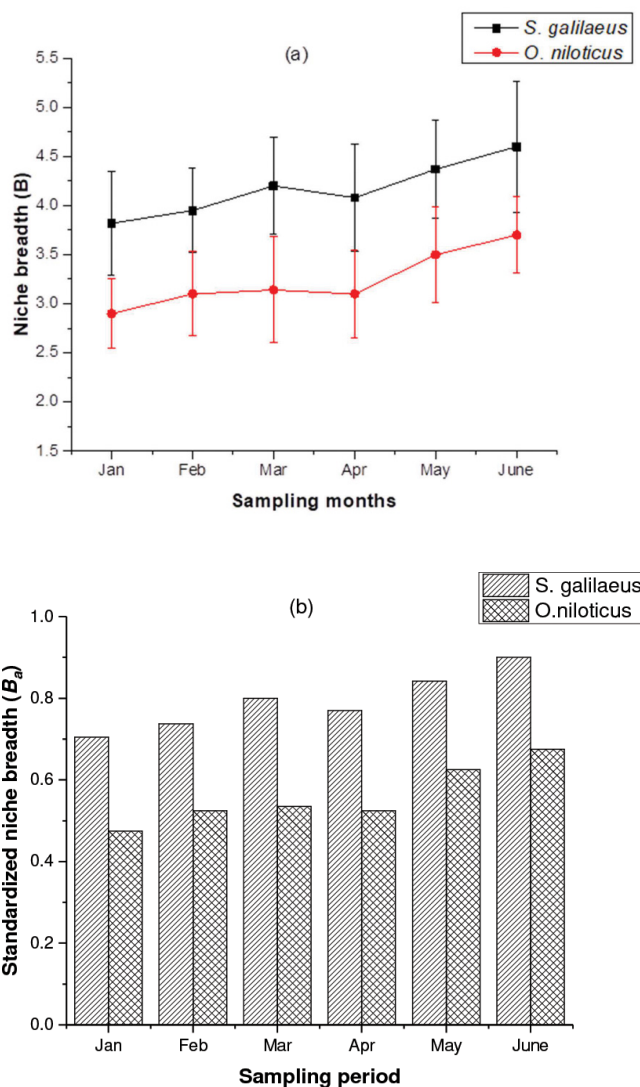

Fig 4. Seasonal variation of (a) trophic niche breadth (Error bar= standard deviation of means) (t-test $p < 0.05$) (b) standardized niche breadth for *S. galilaeus* and *O. niloticus* in Lake Geriyo

for difference in monthly mean trophic niche breadth showed no significant difference (t-test, p<0.05) (Fig. 4a). The standardized niche breadths (B_a) analysis revealed a B_a range of 0.48-0.68 for *O. niloticus* and 0.7-0.90 for *S. galilaeus* (Fig. 4b). Using the modified Grossman (1986) classification of niche breadths, *O. niloticus* was categorized to have an intermediate niche breadth, while *S. galilaeus* was classified as having a high niche breadth.
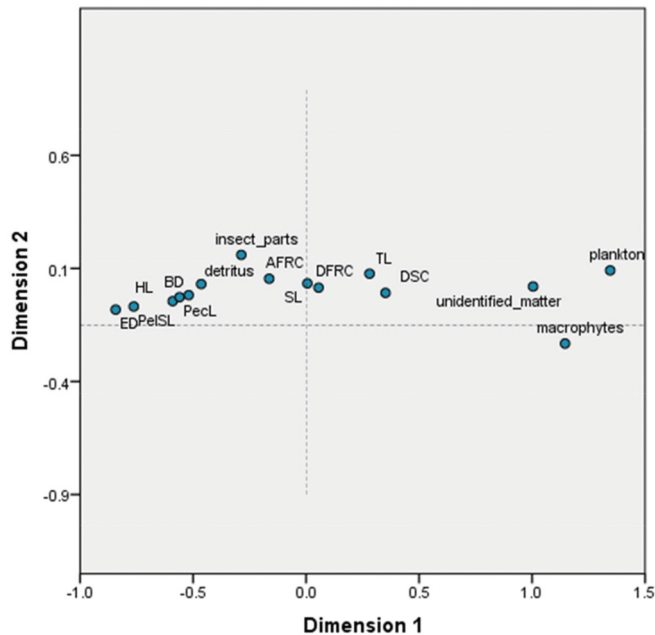

Fig 5. Principal Coordinate Analysis (PCoA) biplot of diet and morphological variables of *Sarotherodon galilaeus* and *Oreochromis* niloticus in Lake Geriyo: where HL (Head length), PecSL (Pectoral spine length), PelSL (Pelvic Spine length), ED (Eye diameter), BD (Body depth), AFR (Anal Fin Ray), DS (Dorsal spine), DR (Dorsal ray), SL (Standard length), TL (Total length)

Trophic/diet overlap index

Mean diet overlap between *S. galilaeus* and *O. niloticus*, according to calculations from Pianka's index, was 0.98, indicating a very high overlap between species.

Principal coordinate analysis

The first two axes from PCoA based on morphological variables and five diet categories consumed in Lake Geriyo explained 72.92% of total variation in diet due to morphological features of species (Fig. 5). The first PCoA axis (56.31%) distinguished species according to diet preference in relation to morphology. Dimension 1 (58.42%) shows an association between AFRC (-0.16), BD (-0.52), HL (-0.59), ED (-0.84), DFRC (-0.06), PelSL (-0.76), PecSL (-0.56), SL (-0.01) and TL (-0.28) of *S. galilaeus*, as well as with a diet of insect parts (-0.29) and detritus (-0.46) suggesting that these morphological variables contributed to the ability of this species to exploit these diet resources. Moreover, *O. niloticus* showed a strong association with DSC (0.35) and plankton (1.35) and macrophyte (1.15) diets (Table 3).

Table 3. Final coordinates of Principal Coordinate Analysis (PCoA)

	Dimension	
	1	2
insect_parts	-0.29	0.16
plankton	1.35	0.09
macrophytes	1.15	-0.23
detritus	-0.46	0.03
unidentified_matter	1.00	0.02
TL	0.28	0.08
SL	0.01	0.03
BD	-0.52	-0.02
HL	-0.59	-0.05
DFRC	0.06	0.02
DSC	0.35	-0.01
AFRC	-0.16	0.06
ED	-0.84	-0.08
PelSL	-0.76	-0.07
PecL	-0.56	-0.03

DISCUSSION

Morphological analysis

Ecological behavior, including hydrodynamic tendencies of fish, have been attributed to size attributes (Motta et al., 1995b; Pusey et al., 2000). In our study, the relatively larger body depth of *S. galilaeus* compared to *O. niloticus* infers a lesser capacity for sustained swimming, but is favourable for burst swimming and maneuvering in structured habitats suitable for targeting mobile prey like insects over short distances (Keenleyside, 2012). In other words, *S. galilaeus* in Lake Geriyo is less adapted for pelagic life and more likely to live in concealed environments rather than open water zone of the lake. The abundance of macrophytes in Lake Geriyo has been documented (NIFFR, 2002) which increases the availability of concealed habitat patches within the lake to support the ecological behavior of *S. galilaeus*.

Studies on diet and microhabitat utilization of fish indicated that higher-median fins (dorsal, anal or caudal fins) imply broader and larger surface area fins suitable

to maintain position, as well as maneuver in water adaptively for pelagic lifestyle (Motta et al., 1995a; Keenleyside, 2012). In our case, the higher number of dorsal spines observed for *O. niloticus* in this study implies broader dorsal fin which favours planktotrophic foraging in the pelagic zone (Figure 4). In addition, the longer pelvic spine and larger eye diameter observed for the *O. niloticus* population could be seen as adaptive attributes for pelagic life. Pelagic zone compared to the littoral zone has little or no features to conceal species from predators, thus pelagic species are considered more visible to predators than benthic species (Thetmeyer and Kils, 1995). In such situations, features like increase in spine lengths relative to body size and prevalence of larger eye size within a population are typical responses to local predation pressure (Goatley et al., 2010, Mobley et al., 2011). Longer spines in prey fish have been reported to discourage predation by penetrating the soft tissues of the mouth of a predator causing difficulty in swallowing and ingestion (Mobley et al., 2011). The smaller spine length and smaller eye diameter recorded for *S. galilaeus* suggests that such larger features may be unnecessary, since its demersal preferences and association with beds of submerged vegetation in freshwater lakes (Trewavas, 1983) may suffice to reduce visibility from predators. The presence of carnivorous fish and potential predators of *S. galilaeus* in Lake Geriyo has been documented (Ekundayo et al., 2014).

Stomach content analysis and ecological implications

The occurrence of food materials in the majority (70%) of stomachs of both species indicates that they had considerable access to food of whatever type within the lake. However, the mixed categories of food items (particularly macrophytes and plankton) observed in the majority of the sampled stomachs portray the species as trophic generalists. In the light of the optimal foraging theory, such occurrence of mixed food categories in stomach contents including alternative dietary materials (sometimes less profitable) are very probable when the density of the preferred (more profitable) food type falls below a critical threshold (Kamil et al., 2012; Charnov, 1976; Schoener, 1987). Thus, the generalist feeding strategy portrayed by the tilapiines in Lake Geriyo could be attributed to low or fluctuating food density. Similar compliance with the optimal foraging theory has been documented for tilapiine cichlids inhabiting a freshwater lake (Oueda et al., 2008). A high occurrence of a particular food category in stomach content may be attributable primarily to resource availability rather than prey selection (Adite and Winemiller, 1997). Thus, the high percentage co-occurrence of both plankton and macrophytes in all stomachs analyzed for both species may be a reflection of the relative availability of these food resources in the lake. More importantly, it highlights a dietary constraint that necessitated the intake of plankton diet to complement the intake of macrophytes. Taken further, it implies that

macrophytes are in limited supply within Lake Geriyo. Macrophyte presence and abundance in lakes directly controls niche availability and ecological opportunities by increasing the habitat complexity and the overall ecosystem productivity(Jeppesen et al., 2012; Vejříková et al., 2017), as such the limited supply of macrophytes in Lake Geriyo suggests that it may be a niche-limited environment.

Trophic niche breadth and dietary overlap analysis

Niche similarities between closely related species in a habitat often result from sharing or harnessing the same resource (Martin and Genner, 2009). Although the niche breadth and standardized niche breadth values of both tilapiine cichlids indicate that they are both trophic generalists, the smaller niche breadth of *O. niloticus* compared to *S. galilaeus* indicates that they are generalists to different degrees. Coexisting trophic generalists having different niche breadths within lake habitats have been reported (Oueda et al., 2008) and could be attributed to constraints imposed by different morphology of each species (Santos-Santos et al., 2015; Hulsey et al., 2013).

The increase in niche breadth with progress from dry season to rainy season (Figure 3a) may be attributed to reduced interspecific competition due to slightly more diversified resources resulting from rains and overflow of the River Benue into the lake during high tide. Similar increased niche breadth in fishes of lake habitats, due to high tides of the wet season, have been documented (Laleye et al., 1995; Oueda et al., 2008).

The formation and occurrence of niche-limited environments, as indicated by the high trophic overlap, have been attributed to a number of factors including anthropogenic impacts and perturbations within natural environments (Carroll et al., 2015; Tilman and Lehman, 2001). Such impacts, including infiltration of agrochemicals into the lake and catchment erosion, and modulated physicochemical properties have been reported for Lake Geriyo (Ezekiel et al., 2015; Shinggu et al., 2015; Yaduma, 2009). It is important to note that such altered habitat conditions could have affected the availability of diverse food resources (specifically macrophyte and macro-invertebrate abundance) (Osborn, 2005; Orwa et al., 2013). Such reduced abundance of food organisms reduce niche availability and ecological opportunity for diet specializations, eventually leading to an increased occurrence of generalist species and fewer trophic guilds (Casatti et al., 2009; Alexandre and Esteves, 2010).

There are evidences that fish assemblages could organize into trophic guilds in order to maximize limited ecological resources (Bonato et al., 2012; Leonard and Orth, 1988). From this study, the high trophic overlap and similar niche breadths observed in our two tilapiine cichlids suggest that both species belong to the same trophic guilds (Bonato et al., 2012). Membership of the same trophic guild may explain the successful coexistence of *S. galilaeus* and *O. niloticus* through resource partitioning within Lake Geriyo.

CONCLUSION

This study uses the relationship between fish morphology and stomach content to infer food availability and diet constraints of two tilapias within a freshwater lake, Geriyo. Although the morphological differences between the tilapias depict the potential for specialized trophic tendencies, similar percentages of more than one food-type in stomach content of both tilapias indicate generalist trophic tendencies. The generalist tendencies may be a product of limited food resources within the lake. The alignment of high diet overlap between the two tilapias and the possibility of limited food availability in Lake Geriyo is consistent with the optimal foraging hypothesis which predicts that increased trophic breadth and diet overlap is observed in situations of low resource abundance/availability. The successful coexistence of *Sarotherodon galilaeus* and *Oreochromis niloticus* despite limited resources within Lake Geriyo indicates suitable partitioning of available food resources.

SAŽETAK

MORFOLOŠKE RAZLIKE I RASPON TROFIČKE NIŠE *Sarotherodon galilaeus* I *Oreochromis niloticus* IZ JEZERA GERIYO, SJEVERNOISTOČNA NIGERIJA

U radu je istraživana povezanost između morfoloških osobina i ishrane dviju jedinih tilapijskih ciklida *Sarotherodon galilaeus* i *Oreochromis niloticus* u jezeru Geriyo, u sjeveroistočnoj Nigeriji. Analizirani su sadržaji želudca 504 jedinki kako bi se morfološke razlike svake vrste povezale s preferencijama ishrane. Izmjereno je jedanaest ekoloških relevantnih morfoloških varijabli, uključujući totalnu duljinu, standardnu duljinu, duljinu glave, dubinu tijela, promjer oka, dužinu prsne peraje, dužinu trbušne peraje, broj mekanih žbica leđne peraje, broj tvrdih žbica leđne peraje i broj žbica analne peraje te su podvrgnute analizi glavnih koordinata (PCoA) u svrhu povezivanja morfoloških razlika svake vrste s njenim preferencijama ishrane. PCoA (korištenjem euklidske udaljenosti) indicirala je veliku morfološku udaljenost između vrsta, ukazujući na prilagodbu različitim prostornim i vertikalnim razdiobama unutar jezera. Nadalje, korelacija morfoloških razlika, s pojedinim kategorijama ishrane ukazuje na potencijal specijalizirane trofičke tendencije, međutim, visoka pojavnost dviju glavnih vrsta hrane (makrofiti i plankton) u sadržajima želuca obiju vrsta, ukazuje na opće trofičke tendencije. Dok je za obje vrste zabilježen visoki trofički indeks preklapanja (0,98), raspon trofičke niše bio je veći kod *S. galilaeus* (4,18 ± 0,32), u usporedbi s *O. niloticus* (3,33 ± 0,24). Usprkos velikim morfološkim razlikama, visoka trofička preklapanja ukazuju na ograničen izbor hrane u jezeru Geriyo. Osim toga, uspješna koegzistencija tilapija u uvjetima ograničenih izvora hrane upućuje na skladnu podjelu hrane u jezeru.

Ključne riječi: Trofička sklonost, morfološka značajka, ishrana, *Sarotherodon galilaeus*, *Oreochromis niloticus*

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