Diving Deep: The Influence of Fish Characteristics on Lake Depth Occupancy

BIOL*4110 - Ecological Methods

Group 4:

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Introduction

Lake depth significantly influences aquatic ecosystems, impacting fish health, longevity and distribution. (McFarlane, 2023). Deeper bodies of water often display stratification, forming distinct thermal layers that can provide unique habitats and influence ecosystem diversity (Rawson, 1952). Habitat choice is shaped by factors such as habitat preference alleles, natal experience, and self-assessment of phenotype suitability for specific environments (Camacho & Hendry, 2020). Finding a suitable environment increases individual performance, and promotes local adaptation (Camacho & Hendry, 2020).

Fish distribution along depth gradients is influenced by ecological niches and habitat specializations. Species inhabiting deeper zones, for instance, tend to exhibit narrower niche breadths and higher degrees of specialization to thrive under the unique environmental pressures of these habitats (Jankowski et al., 2015). These adaptations allow them to take advantage of less competitive, more demanding areas that other species cannot effectively exploit.

Depth significantly influences fish distribution and ecological strategies due to variations in environmental pressures such as temperature, oxygen availability, and predation risk (Chavarie et al., 2018). As depth increases, temperatures drop, favouring adaptations that promote thermal energy conservation, such as body sizes with a higher surface area to volume ratio (Favilla et al., 2023). Moreover, deeper waters require greater energy conservation due to colder temperatures, reduced food availability, and increased pressure, which create resource-scarce and metabolically challenging conditions (Chavarie et al., 2018; Drazen & Seibel, 2007). Therefore, more streamlined body shapes and methodical swimming styles may be advantageous in these environments. Additionally, reduced shelter availability at greater depths can influence rearing strategies. Mouth-brooding species may thrive due to reduced egg predation risks but could face challenges from oxygen constraints and susceptibility to hypoxia (Yanagisawa & Ochi, 1991; Corrie et al., 2007). These ecological demands and adaptations may influence habitat occupancy by depth.

The African Great Lakes, among the world's largest and most biodiverse lakes, are essential for global food resources. Their stratification creates unique depth-driven ecoregions (MacIntyre, 2012). These lakes, home to abundant cichlid species, offer an ideal setting to study depth-related distribution and diversity (Turner et al., 2008).

While studies have explored how environmental gradients such as temperature and oxygen influence fish distribution, there is limited research on how specific morphological and behavioural traits such as body shape and rearing methods interact with these gradients to determine depth preferences (Chavarie et al., 2018). Furthermore, the role of swimming style in conserving energy under the unique pressures of deeper habitats remains poorly understood. The African Great Lakes, with their extreme depth gradients and diverse fish populations, offer an ideal opportunity to explore these relationships. By investigating how traits like body length, shape, rearing method and swimming style correlate to depth, our study aims to address gaps in understanding how fish characteristics influence its residing depth in diverse aquatic environments.

This study investigates how fish traits—body length, shape, rearing method, and swimming style—correlate with depth in the African Great Lakes. First, we hypothesize that body length is correlated with lake depth due to changes in thermoregulation, predicting that as body length increases, so will the lake depth at which they reside. Second, we hypothesize that body shape is correlated with lake depth due to environmental pressures, predicting that more elongated fish are better suited for deeper habitats. Third, we hypothesize that rearing method correlates with depth, predicting that mouth brooders are either more common in deeper waters due to reduced shelter availability for externally laid eggs or less common due to hypoxia risks. Last, we hypothesize that swimming style is correlated to lake depth due to energy conservation, predicting that energy-efficient swimming behaviours are more prevalent among fish inhabiting deeper environments.

Methods

Data Collection

To conduct our study, we collected data from a few different sources, the primary one being fishbase (Boettiger et al., 2012). Within fishbase, we utilized the ‘species’, ‘swimming’ and ‘reproduc’ tables to acquire our needed variables. Additionally, we collected the fish species present in each of the seven African Great Lakes from fishbase, along with their max body length measurements. Both total length (head to tail tip) and standard length (head to base of tail) were included in the collection. To supplement this data, the FISHMORPH database was also included, primarily for additional species max lengths (Brosse et al., 2021).

Within the datasets, we selected max length, body shape, swim mode, and fertilization type as variables to represent each of our hypotheses. After running into gaps with the latter variable, various sources were used to find data on individual fish species (AquaInfo; Chibi-Aquarium; Fishpedia [a-b]; Marine Life Identification [a-e]; Ron’s Cichlids; Roxy Aquarium; Sam Borstein’s Cichlids; Satoh et al., 2022; Seriously Fish [a-c]; Wikipedia).

Data Filtration

Once all the required data was collected, each dataset was compiled into RStudio. Data was merged into four new datasets, one per variable. Each new dataset contained the common factors of genus, species, continent, lake and depth range. Once merged, each dataset was then filtered to contain the previous factors as well as its relevant variable – max length, body shape, swim mode, or fertilization type. Once the variables were selected, the four datasets were further filtered to include only Africa, as well as to omit NAs from the depth range variable. Under the max body length dataset, standard length data points were removed, to maintain measurement consistency. In the body shape dataset, “elongated” and “eel-like” data points were combined into “elongated / eel-like”, to encompass all long body shapes. The datasets were then joined into one dataset containing each of the variables needed for analysis.

Model Fitting & Statistical Analysis

To analyze the effect of each variable, two linear regression models splitting the four of them were created, each being tested against depth. The full models, ‘Depth ~ Body Length + Body Shape + Swim Style’ and ‘Depth ~ Body Length + Body Shape + Rearing Type’ (where rearing represents the fertilization data variable), were created as objects. The R package MuMIn (Barton., 2024) was then used to create the best fitting models for the data using the function ‘dredge’. The dredging provided four best fit models, which are as follows: a) ‘Depth ~ Body Length’, b) ‘Depth ~ Body Shape + Body Length’, c) ‘Depth ~ 1’, d) ‘Depth ~ Body Shape’. The AIC values of models (a) and (b) were indistinguishable, rendering them equally as well fitting as the other. Linear regression tests were run using those top two models to determine statistical significance. Finally, the R package visreg (Breheny & Burchett., 2017) was then used to plot the independent residuals of each variable from the linear regressions.

Results

Dredge Results

After performing the dredge, the results showed that swimming style and fertilization type were not included in any of the top models. This means that including those factors added unnecessary complexity to the model. Body shape was included in two models and max length was included in all of the best models. From this, it was determined that our best models included only max length and body shape data. When looking at the weight value which considers the logLik and AICc values model 5 was found to be the best model (Table 1). Model 7 had very similar results. While model 5 has a better AICc it has a lower logLik when compared to model 7. This means that models 5 and 7 are nearly equivalent in their ability to fit the data. From this, we chose model 7 as our preferred model due to its inclusion of the most variables.

Model	(Intrc)	BdySh	MxLng	df	logLik	AICc	delta	weight
3	72.29	+		4	-515.928	1040.3	8.81	0.007
1	50.11			2	-518.051	1040.2	8.72	0.007
7	48.05	+	0.4775	5	-510.635	1032	0.47	0.436
5	26.74		0.4916	3	-512.62	1031.5	0	0.55

Table 1. Comparison of model fit based on AICc values for different models. The table shows the AICc values for 4 different models, a lower AICc value represents a better fitting model. Models are ordered by increasing AICc values. Models with a delta AICc < 2 are considered to have substantial support.

Model Fitting

Both models 5 and 7 were used to examine the data. Both model results contained significant p-values for max length (Tables 2 and 3). Body shape was not found to have a significant effect on residing depth but has a significant effect on body length.

Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept) 26.7380	10.36	2.581	0.01151	*
MaxLength 0.4916	0.1463	3.36	0.00116	**

Table 2. Result of the linear registration model showing the relationship between residing depth ~ maximum length. The table includes standard error, t value and p value for each predictor. * represent levels of significance.

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	48.0485	14.9082	3.223	0.00179	**
MaxLength	0.4775	0.1457	3.276	0.00152	**
BodyShapefusiform / normal	-31.2851	16.1393	-1.938	0.05585	.
BodyShapeshort and / or deep	-35.2129	43.8582	-0.803	0.42426	

Table 3. **Result of the linear registration model showing the relationship between residing depth ~ maximum length + body shape.** The table includes standard error, t value and p value for each predictor. * represent levels of significance.

VisReg Plots

VisReg plots were used to visualize the individual effects of swimming style, body shape, fertilization, and max length on residing depth, swimming style, body shape, and fertilization showed no trend when compared to residing depth. Max length showed a positive effect on residing depth (Figure 1). From these plots, we can see that fish with different swimming styles and body shapes tend to reside at different depths. Fertilization is not shown to influence residing depth.

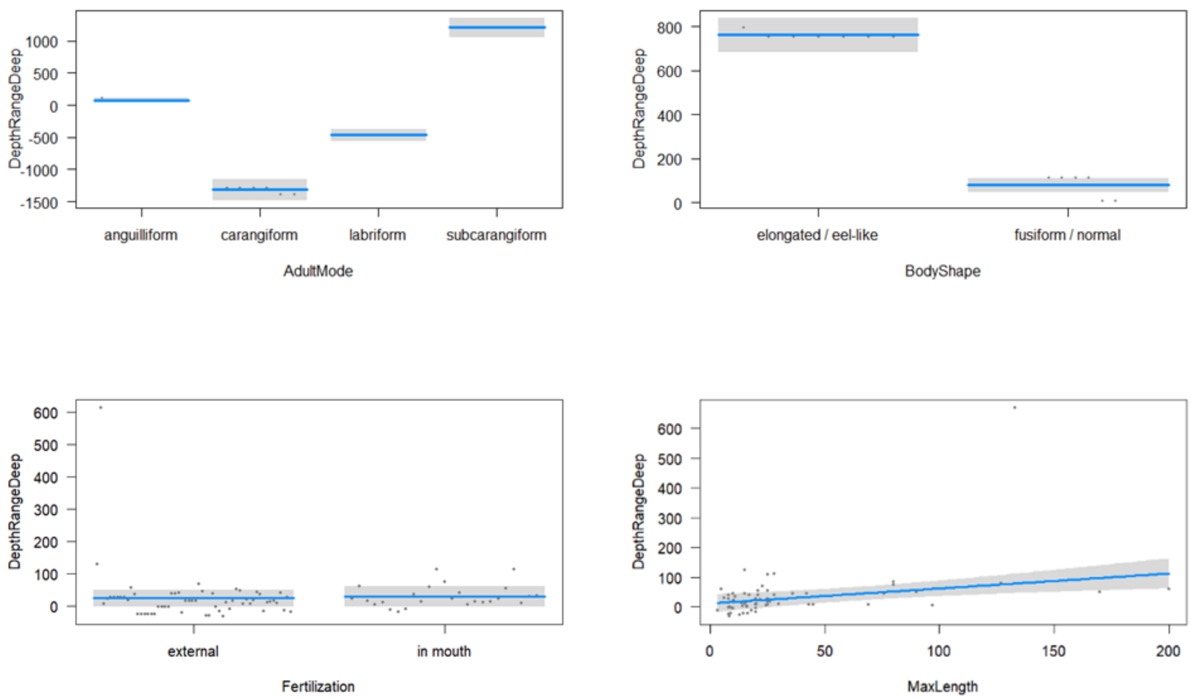

Figure 1. Visreg plots of the effect of swimming style, body shape, and fertilization on fish residing depth based on the fitted linear regression model. The plots show the effect of each predictor on residing depth with the effect of the other predictors held constant. The shaded area represents a 95% confidence interval around the regression line.

Discussion

Rearing Methods

Upon reviewing the results above, the most distinguishable difference from our initial hypothesis and predictions was a lack of significance in whether mouth brooding or traditional egg laying methods would have an influence on the residing depths of their host species. Our original hypothesis, based on studies conducted on *Cichlid* species, suggested that mouth brooding species would reside closer to the surface to allow for greater oxygen availability due to hypoxia and surface respiration methods in female mouth brooding fish (Corrie et al., 2007). Additionally, it was hypothesized that a lack of coverage and shelter in deeper depths could promote mouth brooding in species (Yanagisawa & Ochi, 1991).

A lack of significant data differentiating between the two traits and the residing depths of their associated species could be due to various possible discrepancies in our data, along with the presence of ecological factors playing a more crucial role in determining residing depths. One potential limitation of the study is that all data were collected from the African Great Lakes. Due to the isolation and age of these lakes, many species within are closely related, which could lead to bias in the data due to similar physical and behavioural traits (Lowe-McConnell, 2009).

For example, Lowe-McConnell (2003) demonstrated that the predominant species within the African Great Lakes, particularly Lakes Tanganyika, Malawi, and Victoria, were Cichlid species. This could have masked potential results, as their residing depths might be more strongly influenced by their shared phylogeny and evolutionary past than by whether they are mouth brooders.

Body Length & Shape

Unlike with rearing methods, our original predictions concerning body length were confirmed. Interestingly, body length emerged to display the highest significance in relation to residing depth out of all reviewed traits. This relationship is likely due to the numerous advantages that an elongated body would provide species at lower depths. For instance, increasing body length enhances the surface-area-to-body ratio, aiding thermoregulation in deeper stratifications (Favilla et al., 2023). Additionally, a longer body helps resist increased pressure gradients and reduces drag, conserving energy in nutrient-limited environments (Mindel et al., 2016). Larger body sizes also correlate with greater energy storage, which is beneficial in deeper strata where food availability is sporadic and unpredictable (Lin & Costello, 2023).

Furthermore, longer lengths typically result in an elongated shape, which is linked to feeding strategies that are advantageous and widely adapted to deeper strata such as ambush predation (Claveria & Wainwright, 2014). This aligns with our results, as there was a significant relationship between both body length and body shape, with body shape being the second most important indicator for residing depth. This predictably established a linear relationship between the length of a fish's body and its elongation, reinforcing the importance of these traits in determining depth preferences.

Swimming Styles

A compilation of these two aforementioned factors could also have been interlinked with the swimming styles of the observed species, even if the testing for swimming styles on residing depth was not at the same levels of significance. Our results showed a general trend where carangiform swimming was predominant in deeper-residing species, while subcarangiform swimming was more common in shallower species.

This reinforces our original hypothesis, due to carangiform swimming styles, characterized by the oscillation of the caudal fin with only the rear third of the body moving, being efficient for covering longer distances while conserving energy (Khalid et al., 2021). In contrast, subcarangiform swimming forms utilize a greater portion of the body (~two-thirds from the tail end) to generate propulsion. This allows for more intensive, shorter bursts of speed and maneuverability (Kambe, 2006). The influence of body length and shape could be due to a longer/larger body that allows for greater muscle mass and surface area in the tail, promoting carangiform swimming as it would require less energy for propulsion over longer distances.

Conclusion

Fish length was found to be the most determining factor in influencing residing depths of fish species in the African Great Lakes due to presenting a consistent pattern and high significance across the various species contained within our data. Additionally, the lack of significant results when reviewing rearing strategies' influence on residing depths helps to underscore the importance of considering a broader range of habitats and variables when studying species distribution.

Furthermore, this study is significant in nature as it could be applicable in assisting fisheries with optimizing conditions for greater biomasses of harvested fish. Fish also can act as a bioindicator for aquatic ecosystem health, so establishing baselines for expected physiological traits such as length, and behavioural traits akin to depth range, could help provide a baseline for surveys. For example, larger and longer fish are often linked to more stable and healthy ecosystems, while smaller and growth stunted fish indicate environmental stressors such as pollution and habitat degradation (Whitfield & Elliot, 2002; Okwuosa et al., 2019).

Further research can build upon the results established within this study to explore the evolutionary mechanisms and environmental pressures that have the greatest influence in driving morphological adaptations of longer and elongated bodies in species residing in lower strata, along with reviewing if the established trends are applicable to a broader range of aquatic ecosystems.

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