

Comparative Morphometric Analysis of a Salinity-Tolerant Nile Tilapia (*Oreochromis niloticus*) Local Strain (*Salina*) and Its Parental Strains

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Abstract

This study focuses on the morphology of the Nile tilapia local strain (*Salina*), a salinity-tolerant tilapia hybrid strain developed by crossbreeding between female Nile tilapia *Red NIFI* with male Nile tilapia *Sultana*. The research aimed to analyse the morphometric characteristics of the *Salina* strain to understand species adaptation to suboptimal environmental conditions compared with the parental groups. A total of 60 Nile tilapia fish, ten female and ten male samples from each strain (*Salina*, *Sultana*, and *red NIFI*), were measured for their total length (TL), standard length (SL), head length (HL), body width (WID), dorsal fin length (DL), caudal fin length (CL), pectoral fin length (PL), caudal peduncle depth (CPD), eye diameter (ED), snout length (SNL), and body weight (BW). Each measurement parameter was then normalized by comparing it with the standard length (SL). The data were analysed using MS Excel 2019 and R v4.5.1 for all statistical analysis including MANOVA, Canonical Variance Analysis, Principal Component Analysis, and Hierarchical Clustering Analysis. Condition factor (K) and length-weight relationship (LWR) were calculated to investigate growth conditions and allometric growth patterns, respectively. Based on the findings, the six tilapia populations exhibit overlapping morphological traits, except for female *Salina* with slight differences in morphological variations. This implies its potential unique traits acquired from crossbreeding between two different strains. Meanwhile, male *Salina* showed morphometric traits closely aligned with its male parent, the *Sultana* strain. The condition factor across all populations indicates favourable growth conditions, although the negative allometric growth pattern suggests that length increases more rapidly than body weight, implying an adaptive trade-off in suboptimal environments.

Keywords: adaptation, crossing, morphometric, tilapia, populations

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INTRODUCTION

Aquaculture is one of the most promising sectors within Indonesia's fisheries industry (16.96 million tons in 2023), surpassing the capture fisheries outputs and establishing aquaculture as the primary contributor to the national fish supply. Although annual production varies, the aquaculture sector has sustained a healthy average growth rate of 2.65% from 2019 to 2023. Indonesia's aquaculture industry is marked by its species diversity, encompassing fish, shrimp, and seaweed, which underscores its adaptability and growing economic importance (MMAF, 2024).

Nile tilapia (*Oreochromis niloticus*) is a major aquaculture commodity in Indonesia. In 2023, national tilapia production of Nile tilapia reached 1.36 million tons- the second-highest aquaculture product after seaweed (Albani *et al.*, 2023; Gustiano *et al.*, 2023; MMAF, 2024). Originally native to Africa, Nile tilapia has been successfully introduced to tropical and subtropical regions worldwide (Shuai and Li, 2022). The species is favoured for its rapid growth, high fecundity, and adaptability to suboptimal environmental conditions (Kurniawan *et al.*, 2023; Munguti *et al.*, 2022). Its euryhaline nature allows it to thrive in a wide range of salinity levels, making it suitable for brackish

water culture. Furthermore, Nile tilapia can grow and reproduce in salinities from 0 to 20 parts per thousand (ppt), and can tolerate salinities up to 35 ppt (Diego *et al.*, 2023; Nurchayati *et al.*, 2021).

Several strains of Nile tilapia are cultured in Indonesia, each with specific enhancements or adaptations. These strains include the Bogor Enhanced Strain Tilapia (BEST), the Genetically Enhanced Supermale Indonesian Tilapia (GESIT), the Salinity Resistant Improvement from Sukamandi (*Srikandi*), Nila Ras Wanayasa (NIRWANA), Jatimbulan, the superior Salabintana (*Sultana*), and the National Inland Fish Institute (*Red NIFI*) (Faqih *et al.*, 2015; Nugroho *et al.*, 2024; Taukhid *et al.*, 2024). Among these advancements, the Saline-Tolerant Indonesian Tilapia (*Salina*) represents a significant milestone in selective breeding. This strain was officially released by the Ministry of Marine Affairs and Fisheries in March 2014, according to Decree Number 22/KEPMEN-KP/2014 (Dewi *et al.*, 2018).

The *Salina* strain (*O. niloticus*) was developed through crossbreeding between female *Red NIFI* (*O. mossambicus* × *O. niloticus*) and male *Sultana* (*O. niloticus*) (Figure 1), both were from a certified Main Center of Freshwater Aquaculture (MCFA) Sukabumi, West Java, Indonesia (Aliah, 2017). This center obtained the Indonesian Good Aquaculture Practices (IndoGAP) certificate that the fish seed produced is of high quality. IndoGAP is a set of guidelines and procedures for breeding fish, including broodstock management, spawning, egg hatching, and larval/seed maintenance in a controlled environment, by applying technologies that meet technical, management, food safety, and environmental criteria and requirements.

The *Salina* strain spawning is conducted in a brackish environment, ensuring the hybrid *Salina* fry is highly adaptable to such conditions. Fish crossbreeding occurs naturally or artificially between different species and strains to produce superior new strains. The *Salina* strain exhibits notable characteristics, including high tolerance to salinity levels exceeding 20 ppt, high survival rates, a low feed conversion ratio (FCR), and a strong resistance to pathogenic bacteria from

Streptococcus species. These conditions emphasize the *Salina* strain as a highly promising candidate for revitalizing aquaculture systems, particularly in inactive shrimp ponds and freshwater ponds affected by saline intrusion due to rising sea levels. By leveraging the resilience and adaptability of the *Salina* strain, these ponds may overcome salinity-related challenges to resume sustainable operations, contributing to food security and local economies (Dewi *et al.*, 2018; Setyawan *et al.*, 2022).

Fish morphometrics is a critical technique used in ichthyology to quantitatively assess the physical dimensions of fish, such as the length, height, and other key body measurements. These measurements are essential for identifying and comparing morphological variations both within and between species or populations. Morphometric analysis plays a vital role in understanding phenotypic variation and adaptive traits, providing insights into environmental factors response (Tripathy, 2020). Moreover, morphometric analysis also contribute to broader ecological and evolutionary studies by revealing patterns in fish morphological divergence. Numerous studies have extensively documented the morphometric characterization of various Nile tilapia species across diverse environmental conditions (Kosai *et al.*, 2014; Ndiwa *et al.*, 2016; Kwikiriza *et al.*, 2023; Engdaw, 2023).

However, a notable gap persists in the literature regarding the morphometric properties of saline-tolerant Nile tilapia strains. To address this gap, this study investigates the morphology and morphometric characteristics of the hybrid *Salina* strain, developed from a crossbreeding between female *Red NIFI* (*O. mossambicus* × *O. niloticus*) and male *Sultana* tilapia. By establishing baseline data on the morphology of these hybrids, the study aims to provide insights on their adaptability and potential applications in aquaculture. Additionally, comparative analysis the hybrid offspring and their parental strains are expected to yield valuable contributions to fisheries biology, offering insightful information on the effects of hybridization on fish morphology, especially in suboptimal environments.

MATERIALS AND METHODS

Ethical Approval

This study did not involve animal experimentation. Fish were obtained from routine aquaculture production at the Regional Technical Implementation Unit in Karawang, West Java, Indonesia. All individuals used were already harvested and frozen before morphometric analysis. According to institutional and national regulations, ethical approval was not required for studies involving post-mortem morphometric measurements of fish.

Study Period and Location

All fish in this study were collected at the Regional Technical Implementation Unit in Karawang, West Java, Indonesia (6°04'06.4"S and 107°25'06.7"E). This study was performed from 2011 to 2012.

Fish Rearing Location and Conditions

The 3 tilapia strains: *Red NIFI*, *Sultana*, and *Salina* were reared in different earthen ponds, with males and females separated by 3x5m² hapas within each pond. All reared fish were fed with uniform commercial feed (32% protein content) twice a day (*at satiation*). During the rearing period, water quality was measured periodically. Water quality records showed similar trends in all ponds: temperature 27.8–32.7 °C, salinity 5–10 ppt, pH 7.16–8.92, dissolved oxygen 6.65–8.54 mg/l, turbidity 3.29–4.35 NTU, and Ammonia (NH₃) 0.18–0.73 mg/l. These values are considered normal and suitable for aquaculture performance.

Sample Collection and Morphometric Measurement

The fish samples were obtained in frozen form from a routine harvest at the Regional Technical Implementation Unit in Karawang, West Java, Indonesia. Within each pond, females (10 samples) and males (10 samples) from each strain of *Red NIFI*, *Sultana*, and *Salina* in different ponds were collected randomly. Fish collected in this study were more than 6 months old and considered in the adult stage (Ariyanto,

2002). With a total of 60 fish, only a single trained individual was assigned to take morphometric measurements using a Mitutoyo Vernier Caliper with a precision of 0.01 cm, while the body weight was determined using a calibrated digital scale with an precision of 0.01 g. The fish total length (TL), standard length (SL), head length (HL), body width (WID), dorsal fin length (DL), caudal fin length (CL), pectoral fin length (PL), caudal peduncle depth (CPD), eye diameter (ED), snout length (SNL), and body weight (BW) were used for morphometrics data (Figure 2).

Data Analysis

Each measurement parameter was then normalized by comparing it with the standard length (SL) before any statistical processing as displayed in Table 1 to ensure consistency across all measurements. This approach enabled fairer group comparisons, ensuring morphometric differences reflected biological variation rather than age, growth, or environmental influences (Ramli, 2016). The data was processed and analysed using MS Excel 2019 and R v4.5.1 for all statistical analysis. The normalized data were checked for normality and homogeneity assumptions with Shapiro–Wilk and Levene's test, respectively. Multivariate Analysis of Variance (MANOVA) was performed incorporating strain, sex, and their interaction as factors, and using all 10 standardized morphometric traits as dependent variables. To evaluate pond effects, we conducted PERMANOVA with permutations restricted within pond blocks (*Red NIFI* in pond 1, *Sultana* in pond 2, and *Salina* in pond 3).

Following the multivariate results, we conducted univariate ANOVAs with Tukey's post-hoc tests to identify which specific traits contributed most to the observed difference. Partial eta squared (η_p^2) was used to investigate the effect sizes of *strain*, *sex*, and *strain*×*sex* using Cohen's benchmark for interpretation. Principal component analysis (PCA), canonical variance analysis (CVA), and hierarchical clustering analysis (HCA) were employed to evaluate variation, relationship, and correlation

between fish populations among multiple morphometric traits.

The length-weight relationship (LWR) of the samples was analysed to assess growth patterns and overall body condition, using the established standard allometric equation:

$$W = a L^b \dots\dots\dots(1)$$

Where W represents the body weight in grams, L denotes the total length in centimetres, while a and b are the intercept and slope of the regression function, respectively (Le Cren, 1951). This relationship provides insights into growth dynamics and body proportionality, indicating the association of length and weight within the population. Piecewise regression was also investigated as a comparative LWR analysis model in this study (De Robertis and Williams, 2008) which formulated in the equation:

$$\log_e(W) = \log_e(a_i) + b_i \log_e(L) + \varepsilon \dots\dots\dots(2)$$

Where i is an index of the fish group, e is the error term, W , L , a , and b are terms of the allometric equation defined before. Additionally, the condition factor (K), which serves as an indicator of the fish's well-being and robustness, was calculated using the formula:

$$K = 100 \times (W/L^3) \dots\dots\dots(3)$$

Where W is the body weight in grams and L is the total length of the fish in centimetres (Htun-Han, 1978). The condition factor allows for a comparative analysis of fish health across different size classes and environmental conditions, offering valuable data for understanding fish physiological state across the populations. The p -value < 0.05 is considered significant in all analysis.

RESULTS AND DISCUSSION

Morphometric Characteristics of Tilapia Populations

In this study, eleven primary morphometric traits, specifically head length (HL), pectoral fin

length (PL), body weight (BW), body width (WID), total length (TL), standard length (SL), dorsal fin length (DL), and caudal fin length (CL), caudal peduncle depth (CPD), eye diameter (ED), and snout length (SNL). This selection was based on the premise that primary morphometric characteristics include total length (TL) and body weight (BW), as these traits are adequate for assessing fish condition and estimating biomass (Zhang *et al.*, 2024). Targeting these traits enables efficient analysis while preserving accuracy of condition and biomass estimates, supporting practical implementation in fisheries biology.

The sample size of 10 males and 10 females per strain was determined based on practical constraints, including available resources, labor, time, and costs. While we recognize that larger sample sizes generally increase statistical power and the ability to detect small effect sizes, our study prioritized balanced sampling across all strains to enable fair comparisons. Random sampling within each strain was applied to ensure that every individual in the population had an equal chance of being selected, thereby reducing selection bias and increasing representativeness. Although the modest sample size may limit the precision of certain estimates and the detection of subtle morphometric differences, it remains sufficient for detecting moderate to large differences in multivariate morphometric traits, as supported by similar sample sizes in previous tilapia morphometric studies. Future research with larger cohorts and replicated trials would be valuable to confirm and extend these findings. To minimize measurement error, all instruments were regularly calibrated prior to data collection, with particular attention to the digital scale, which was calibrated before each use. Morphometric measurements were conducted by a single trained individual to avoid inter-observer variability. In addition, a subset of samples was randomly re-measured to assess and ensure data precision and consistency.

One-way ANOVA revealed significant standardized morphometric differences among the populations (Table 1). Tukey HSD tests showed that female *Salina* had the lowest TL:SL and CL:SL values, indicating smaller overall

body size and caudal development than both male *Salina* and the parental (male *Sultana*, female *Red NIFI*) and nonparental groups. This smaller body form, also reflected in raw (unstandardized) measurements as shown in Table 2, suggests slower somatic growth, which in aquaculture, which may be influenced by environmental mismatches. According to the official released document by Ministry of Fisheries and Marine Affairs (Keputusan Menteri Kelautan dan Perikanan Republik Indonesia Nomor 22/KEPMEN-KP/2014), the *Salina* strain exhibits optimal growth at salinity levels of 20–25 ppt. Therefore, the lower salinity of 5–10 ppt in the present study, coupled with quite fluctuated water quality conditions in the pond and exposure to unpredictable factors like rain, likely constrained their growth performance. Male *Salina*, while shorter (lower TL:SL) and lighter (lower BW:SL) than male *Sultana* and male *Red NIFI*, exhibited proportionally longer dorsal fins (DL:SL), larger heads (HL:SL), and deeper bodies (WID:SL), indicating possible shifts in growth allocation under suboptimal salinity. In contrast, male *Red NIFI* consistently displayed the largest body proportions among groups, reflecting strong growth potential under pond culture and suggesting suitability for production traits prioritized in aquaculture, such as rapid biomass gain and higher market yield. The smaller body proportions observed in *Salina* compared to its parental lines may have implications for reproductive performance. In many fish species, fecundity increases with standard length and body weight because larger individuals possess greater energy reserves and larger body cavities for oocyte production (Jonsson and Jonsson, 1999). For example, Hasan *et al.* (2020) reported that 55.1% of fecundity variation in *Clupisoma garua* catfish could be explained by variation in standard length, with fecundity rising significantly alongside body size. Given this potential relationship, the reduced body size in *Salina* may limit egg production, representing a potential size–fecundity trade-off. Whether this trade-off arises primarily from hybridization effects or from environmental constraints is unclear, as *Salina* in this study were

reared at 5–10 ppt salinity which is lower than the 20–25 ppt range previously associated with optimal growth.

The findings of this study align with previous research that has indicated significant differences in morphometric traits among various tilapia strains. Allaman *et al.*, (2013) and Regala *et al.*, (2018) emphasized that tilapia strains can exhibit distinct morphological characteristics, highlighting the inherent variability within the species. Similarly, this study also demonstrates significant differences in certain morphological traits among the tilapia strains examined. The observed variation in morphological traits occurs between different strains observed. As mentioned by Ramli (2016), such variation occurs between different strains and within hybrids of the same or different parental strains, suggesting that genetic diversity plays a crucial role in shaping the physical characteristics of tilapia and leading to a wide range of morphometric outcomes. Moreover, this study also align with Wahidah *et al.* (2023), who reported morphological differences between male and female tilapia were influenced by genetic and environmental factors, contributing to the differences in body shape and size between the males and females.

Environment Effects and Strain $\times$ Sex Interaction Analysis

The environment might affect the fish morphometric traits, especially when different tilapia strains are being reared in different ponds as in this study design. While rearing conditions aimed to minimize environmental variation, we acknowledge that strain and pond effects were confounded in this study, and thus environmental influences could not be entirely ruled out. To partially address this, we performed a permutation-based MANOVA with permutations restricted within the pond to control for pond-level variation. These approaches provide valid tests for sex and strain $\times$ sex, while we interpret the strain main effect cautiously as potentially reflecting both genetic and pond influences.

Based on PERMANOVA results, Strain $\times$ sex effects remained high ($R^2 = 0.868$, p -value < 0.05), suggesting that morphological

differentiation was not solely driven by pond-level differences. With this evidence, we have

reasonable means to focus on *strain x sex* interaction analysis.

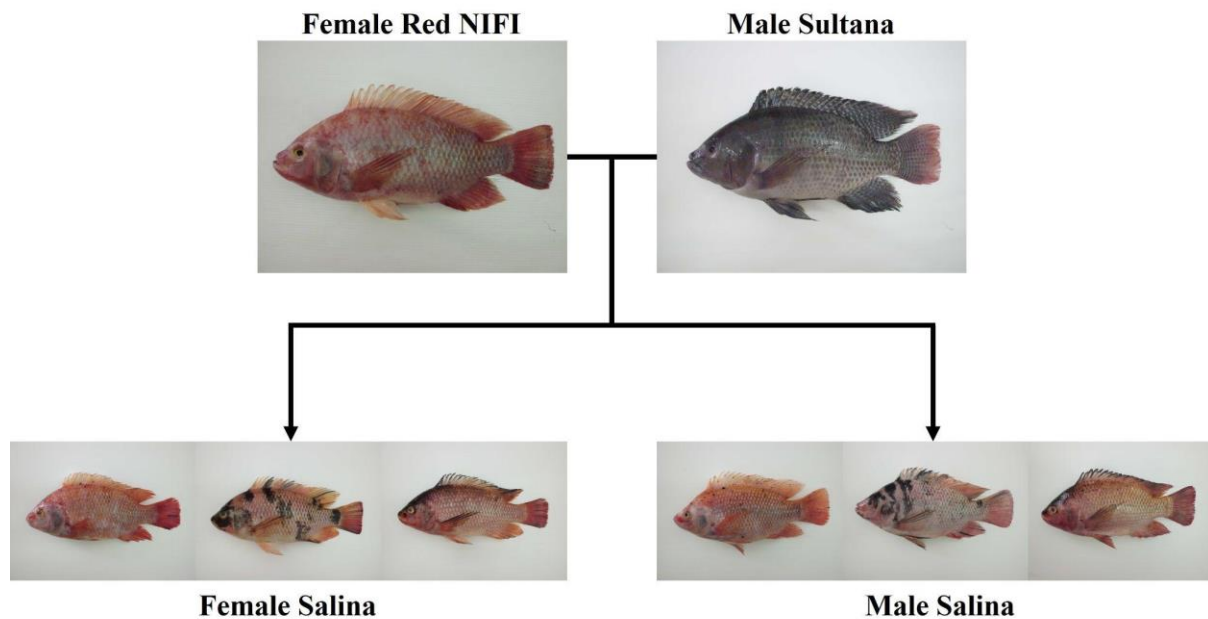


Figure 1. Crossbreeding diagram of *Salina* strain from its parental group: female *Red NIFI* (*O. mossambicus* x *O. niloticus*) and male *Sultana* (Author's documentation).

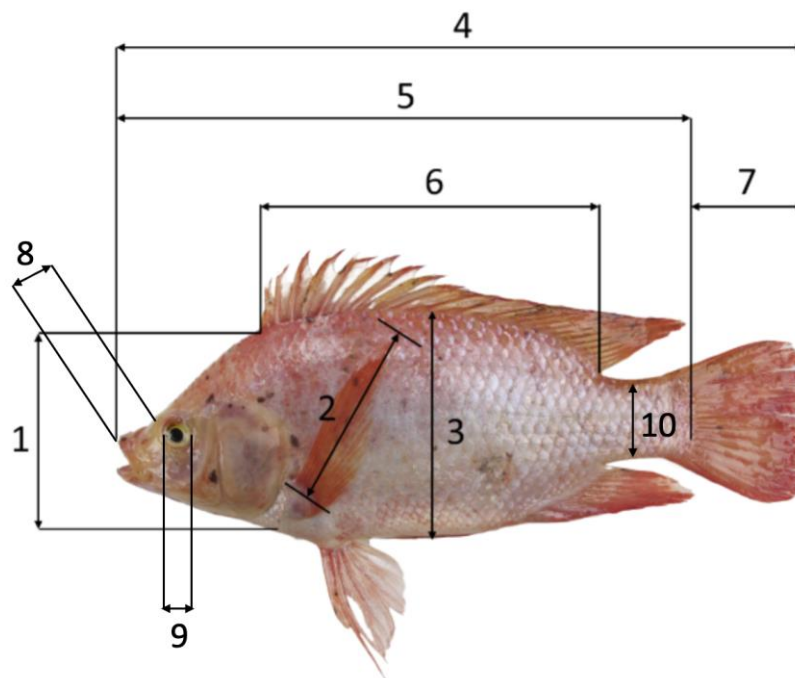


Figure 2. Measurements of the morphometric characteristics of examined *O. niloticus*: 1. head length (HL), 2. pectoral fin length (PL), 3. body width (WID), 4. total length (TL), 5. standard length (SL), 6. dorsal fin length (DL), 7. caudal fin length (CL), 8. snout length (SNL), 9. eye diameter (ED), and 10. caudal peduncle depth (CPD) (Author's documentation).

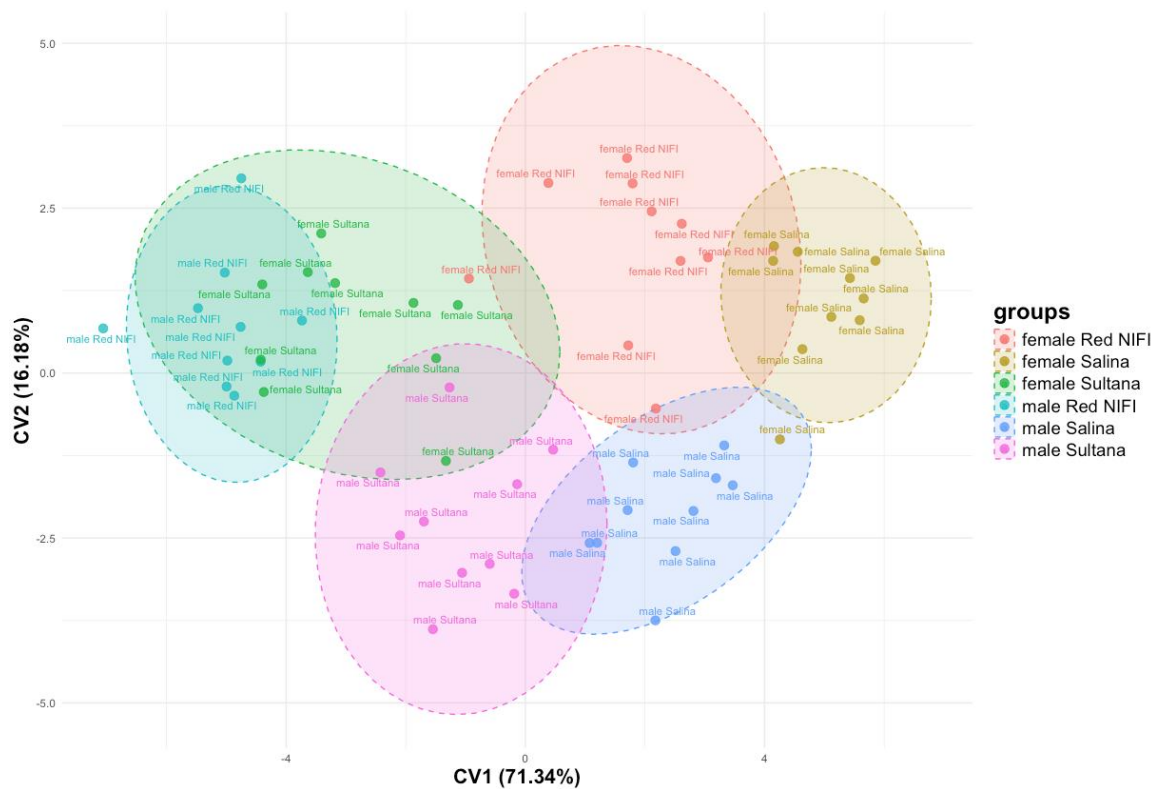


Figure 3. Canonical Variates Analysis of the 6 tilapia populations shows clustering separation between males and females in each strain with CV1 contributing 71.34% and CV2 contributing 16.18% to the variance.

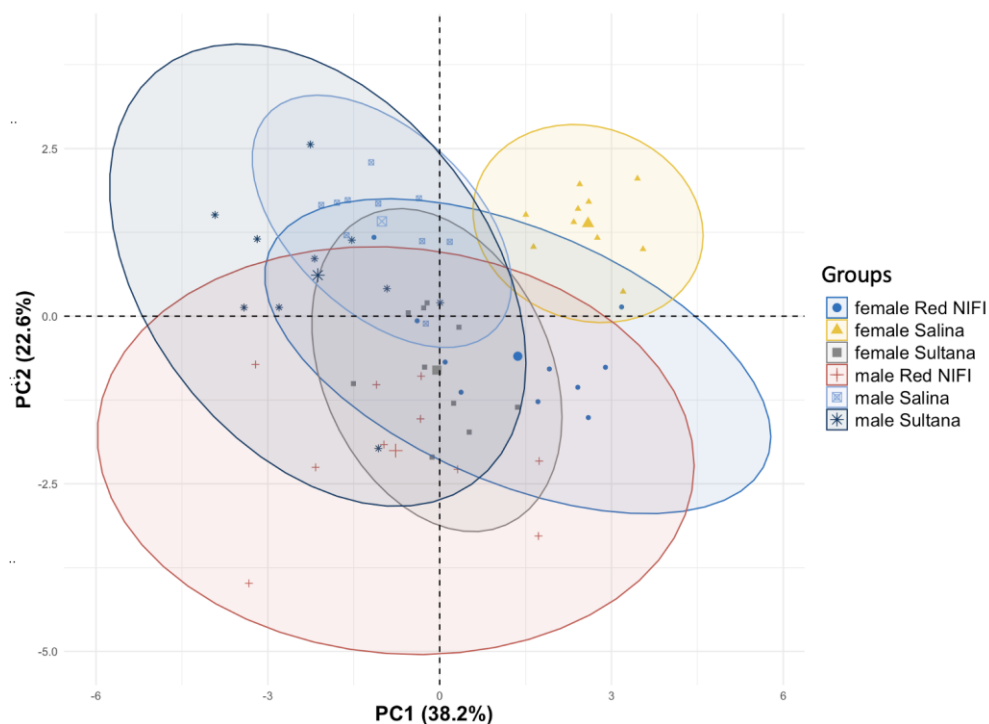


Figure 4. Principal component analysis of the 6 tilapia populations shows overlapping between most of the groups and a distinguished separation of female *Salina*, with PC1 contributing 38.2% and PC2 contributing 22.6% to the variance.

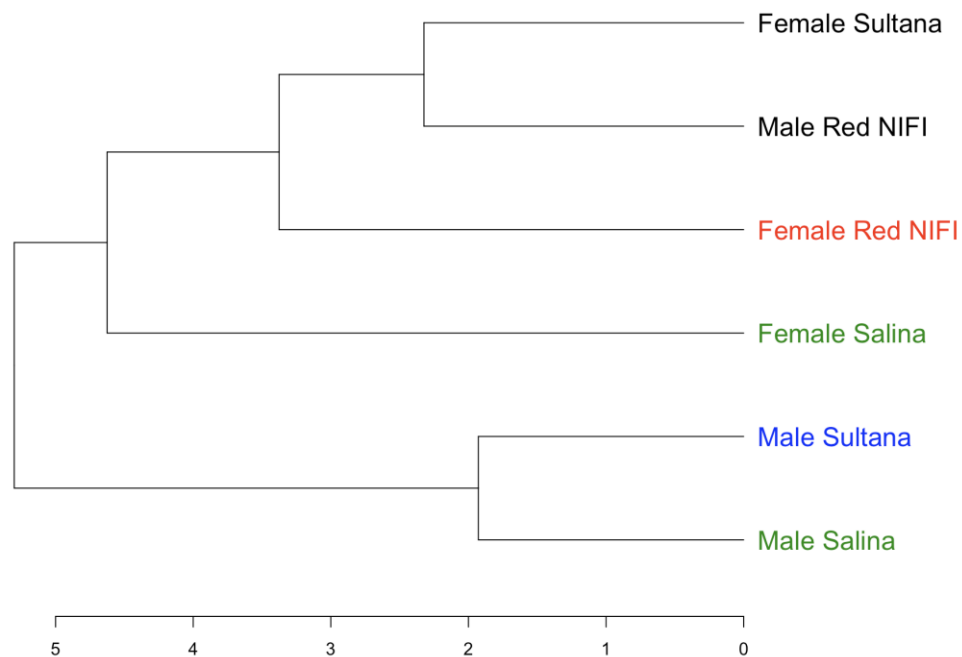


Figure 5. A cluster dendrogram of six tilapia groups based on multi-morphometric traits. Distance metrics and branches show separation between male *Salina* and female *Salina*. Both are closely related to its parental group, where male *Sultana* clustered with male *Salina*, while female *Red NIFI* has a closer distance to female *Salina*.

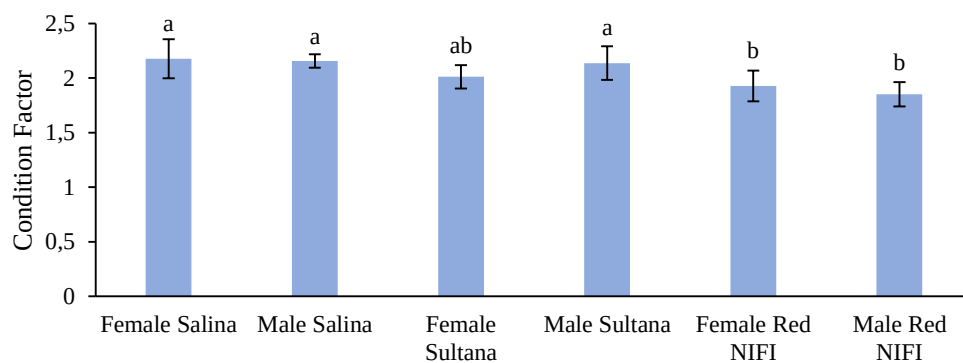


Figure 6. Condition factors (K) of the 6 tilapia groups. Error bars represent standard errors from the total sample, with statistical differences indicated by different letters ($p < 0.05$).

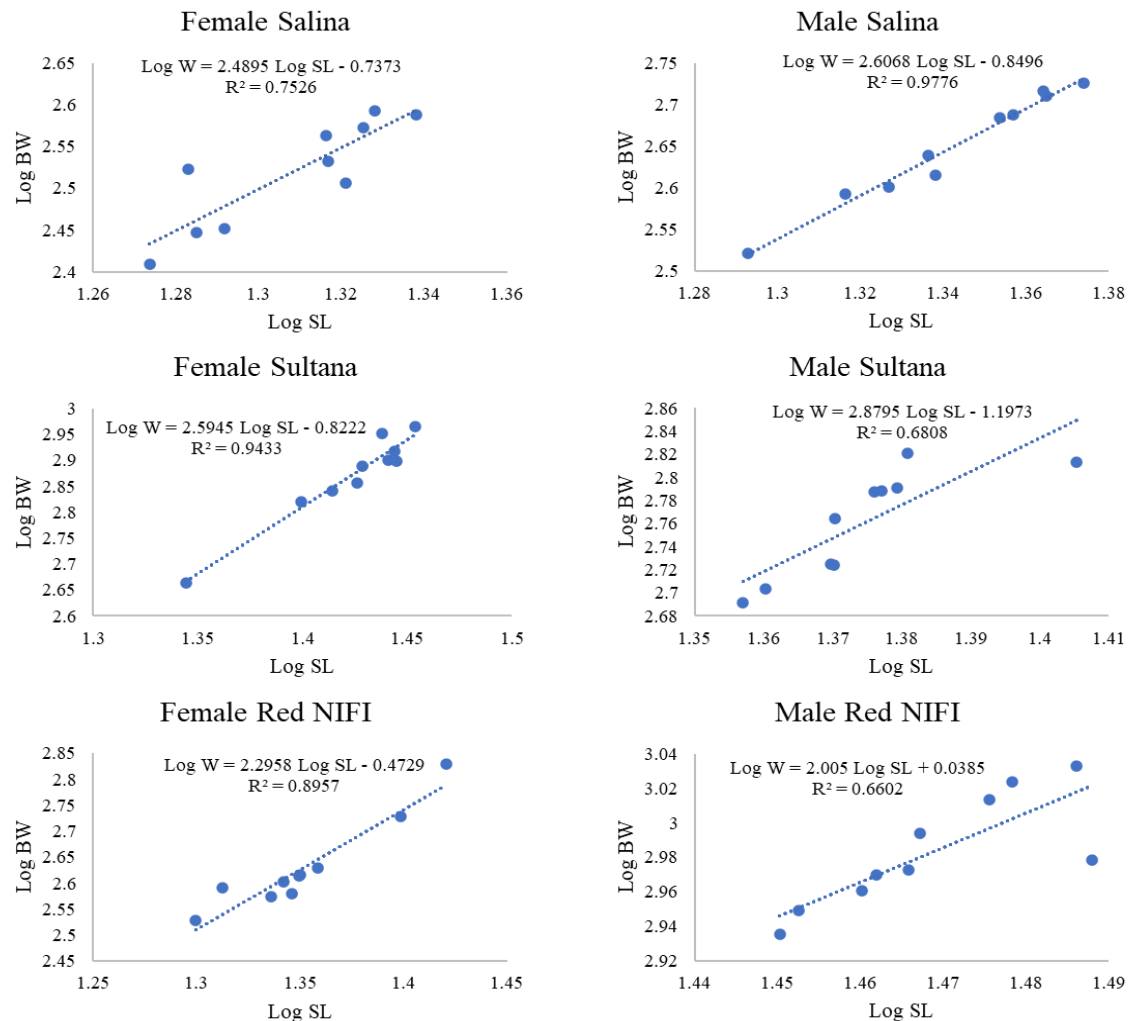


Figure 7. Length-weight relationship (LWR) among the tilapia populations using standard Le Cren's allometric model. R^2 is a coefficient of determination that represents the proportion of variance in the body weight (BW) that can be explained by the standard length (SL).

Based on MANOVA results, there is an interaction between *strain* $\times$ *sex* ($p < 0.05$), suggesting that morphological differences among strains vary by sex and vice versa. Further, two-way ANOVA (Table 3) revealed strong *strain* $\times$ *sex* interactions for standardized BW:SL, ED:SL, CL:SL, and PL:SL ($\eta_p^2 > 0.14$; $p < 0.05$). Adding evidence that morphological traits differ between sexes, and vice versa, that sex differences are strain-dependent, particularly on mentioned variables. Moreover, based on partial η^2 , sex parameters have significantly large effects on several traits such as BW:SL, WID:SL, CL:SL, SNL:SL, TL:SL, HL:SL, CPD:SL, and DL:SL. This implies that sexual dimorphism exists in the populations, hence sex may strongly influence variation in weight and body size of the studied

tilapia populations. Canonical Variates Analysis (Figure 3) visualizes how the males and females in each strain are separated by morphometrical profiles with CV1 contributing 71.34% and CV2 contributing 16.18% to the variances.

Morphometric Relationships between *Salina* Strain and Its Parental Groups

The application of Principal Component Analysis (PCA) in fish morphometric analysis serves as a powerful tool for evaluating the variation and relationships among multiple morphometric traits. By reducing the dimensionality of the dataset, PCA highlights the primary axes of variation while preserving essential patterns, thus facilitating the interpretation of complex trait interdependencies

(Laskar *et al.*, 2013). In this study, PCA was employed to analyze ten distinct morphometric traits, resulting in the extraction of seven principal components. Each component represents a variation aspect present in the original dataset. Notably, the first two principal components (PC1 and PC2) accounted for a substantial portion of the variance, with PC1 contributing 38.17% and PC2 contributing 22.62%, culminating in a combined total of 60.79% of the observed variation (Table 4). Based on PCA loadings, variables of standardized CL:SL, CPD:SL, TL:SL, WID:SL, and HL:SL are most contributed to PC1. Therefore, PC1 represents general body size and caudal propulsion capacity, which may be linked to swimming performance, predator avoidance, or sexual display. Meanwhile, variables of standardized ED:SL, BW:SL, HL:SL, WID:SL, and TL:SL are the main contributors to PC2. This component represents head-sensory morphology which may be related to visual adaptations against water turbidity and light intensity. In addition, eye size might be related to schooling coordination, social cue detection or allometric growth. PC2 also represents body condition related to health and sexual maturity. The cumulative variance explained by the first four components exceeded 60%, indicating that these components retained the critical morphometric information from the original variables, consistent with the thresholds established in previous studies (Yu *et al.*, 1998).

In this study, Principal Component Analysis (PCA) revealed considerable overlapping across all clusters, with the notable exception of the female *Salina* (Figure 4). This distinction suggests notable differences in morphometric traits in female *Salina* implying unique morphometric traits. However, no significant separation was observed between the male *Salina* group and its parental lines, especially this group overlapping closely with male *Sultana*. The lack of distinct separation between male *Salina* and male *Sultana* implies a considerable overlap in their morphometric characteristics, suggesting that the male *Salina*'s traits closely resemble those of their parental lines. This could be attributed to the specific breeding history of these

strains, as the *Salina* strain is a hybrid of male *Sultana* and female *Red NIFI*, and may have inherited distinct traits from both parental lines (Kwikiriza *et al.*, 2023). The overlapping clusters observed in the PCA further reinforce the likelihood that the majority of the fish sampled originate from a common genetic pool, which aligns with the theory that shared environmental pressures or genetic backgrounds can lead to similar physical traits (Le Moan *et al.*, 2021). However, the clear distinction seen in the female *Salina* underscores the presence of significant morphometric variation, likely driven by their unique genetic backgrounds or selective breeding practices. This distinctiveness could have important implications for understanding the genetic diversity and potential breeding strategies of these populations.

Hierarchical cluster analysis (HCA) plays a pivotal role in fish morphometric research, particularly in identifying similarities and differences in morphological characteristics across various populations. This method provides a visual representation of relationships through dendrograms, which depict clusters of individuals or groups based on their morphological traits (Ondang *et al.*, 2019). HCA not only facilitates the identification of distinct morphological groups but also serves as an essential tool in taxonomy, stock structure analysis, and evolutionary studies (Rasheeq *et al.*, 2023). By organizing individuals into hierarchical clusters, researchers can observe patterns that may otherwise remain hidden, offering insights into the biological and ecological significance of these groupings.

In the present study, HCA revealed the formation of two distinct clusters as shown in the dendrogram Figure 5. The first cluster comprised the male *Sultana* and the male *Salina*, while the second cluster included the female *Salina*, the female *Red NIFI*, the male *Red NIFI*, and the female *Sultana*. In the second cluster, female *Red NIFI* and female *Salina* are separated from the nonparental group of male *Red NIFI* and the female *Sultana*. This dendrogram, along with the PCA results, highlights a statistical similarity distance on real biological inheritance between

Salina and its parental strain. It also implies potential maternal effects between female *Red NIFI* and female *Salina*. Not to mention that both male and female *Salina* exhibit a red body color with small portions of dark spots scattered on their body, which is another implication of maternal dominance in *Salina* strain, since female *Red NIFI* exhibit a red body color (Figure 1). Maternal effects can significantly influence traits in tilapia, including body weight, body depth, and fillet weight. These effects arise from the maternal transmission of mRNA transcripts, cytoplasmic elements, and mitochondrial DNA (mtDNA), all of which play crucial roles in early development. Because mtDNA is inherited exclusively from the female, the interaction between mitochondrial and nuclear genomes is known as mitonuclear coevolution, which shapes phenotypic traits such as metabolic rate, growth, and morphology (Quéméneur *et al.*, 2022). Another mechanism is that maternal gene expression can shape offspring phenotype through egg composition, hormone deposition, and the early developmental environment, independent of direct DNA inheritance (Joshi *et al.*, 2020). Another study suggests the larger or better-conditioned females often produce larger eggs with greater yolk reserves, enhancing early larval growth and influencing body shape and size during the juvenile stage (Koenigbauer and Höök, 2023).

The complementary nature of PCA and HCA in this analysis highlights the complexity of the morphometric relationships among the different tilapia groups. While PCA offers a broad, multivariate perspective on trait similarities and differences, HCA provides a more granular view, delineating specific clusters that represent inherent groupings within the data. The integration of both methods allows for a more comprehensive understanding of morphometric variation, which is essential for interpreting the biological and ecological implications of these findings (Silva, 2003). In this study, the PCA revealed substantial morphological overlap among most populations. Notably, male *Salina* overlapped more extensively with male *Sultana* than with female *Red NIFI*. This pattern is

consistent with the HCA, which clustered male *Salina* and male *Sultana* within the same branch, whereas the female *Red NIFI* formed. These results suggest that male *Salina* morphologically resembles its male parent more strongly. In contrast, female *Salina*, while still overlapping with both parental populations in the PCA, exhibited the most distinguishable cluster separation among all groups. The HCA placed female *Salina* closer to female *Red NIFI* and distinctly apart from male *Sultana*, indicating that female *Salina* inherits more morphological similarity from its female parent and shows more differentiated morphometric traits compared to male *Salina*. Taken together, the concordance between PCA and HCA highlights that male and female hybrids express different parental resemblance patterns, reflecting potential sex-linked influences on morphological inheritance. Such detailed analysis is crucial in fisheries research, as it informs conservation strategies, breeding programs, and the management of fish stocks.

Condition Factor and Length-Weight Relationship Correlation

The condition factor is a widely recognized and essential indicator in fisheries science, frequently employed to evaluate the health status, body condition, and growth performance of fish populations in various environments. By examining the weight-to-length ratio, the condition factor provides insight into how well individual fish are thriving, often reflecting underlying biological and ecological conditions. In this study, the condition factor (K) differed among the populations observed ($p < 0.05$), as shown in Figure 6. Both male and female *Salina* groups demonstrated higher condition factors compared to the male and female *Red NIFI* groups, although no significant differences were found when compared to male and female *Sultana* populations. Importantly, all the populations exhibited condition factors greater than 1, which is a key indicator of fish health and overall well-being during culture (Jisr *et al.*, 2018). Numerous factors impact the condition factor, with intrinsic aspects such as sex and developmental stage

Table 1. Standardized morphometric traits of tilapia populations

Populations	TL:SL	DL:SL	CL:SL	HL:SL	WID:SL	PL:SL	CPD:SL	ED:SL	SNL:SL	BW:SL
Female <i>Salina</i>	1.22±0.01 ^d	0.59±0.01 ^{ab}	0.23±0.01 ^c	0.39±0.01 ^b	0.40±0.01 ^{bc}	0.32±0.04 ^c	0.15±0.00 ^a	0.06±0.01 ^{ab}	0.12±0.00 ^d	16.33±1.7 ^e
Male <i>Salina</i>	1.25±0.01 ^c	0.61±0.02 ^a	0.26±0.01 ^b	0.41±0.01 ^a	0.43±0.01 ^a	0.36±0.02 ^{ab}	0.16±0.01 ^a	0.06±0.00 ^{ab}	0.12±0.01 ^{bc}	20.37±1.92 ^d
Female <i>Sultana</i>	1.26±0.01 ^{abc}	0.60±0.01 ^a	0.26±0.01 ^b	0.39±0.01 ^b	0.40±0.01 ^{bc}	0.39±0.02 ^a	0.15±0.00 ^a	0.06±0.01 ^{bc}	0.12±0.01 ^{cd}	28.20±3.37 ^b
Male <i>Sultana</i>	1.27±0.01 ^{ab}	0.60±0.01 ^a	0.28±0.01 ^a	0.41±0.02 ^a	0.43±0.02 ^a	0.38±0.03 ^a	0.16±0.01 ^a	0.06±0.01 ^a	0.13±0.01 ^{ab}	24.41±2.02 ^c
Female <i>Red NIFI</i>	1.25±0.01 ^{bc}	0.58±0.01 ^b	0.26±0.01 ^b	0.38±0.02 ^b	0.39±0.02 ^c	0.35±0.04 ^{abc}	0.15±0.01 ^a	0.06±0.00 ^{ab}	0.12±0.01 ^{cd}	19.12±2.63 ^{de}
Male <i>Red NIFI</i>	1.27±0.02 ^a	0.6±0.01 ^{ab}	0.27±0.02 ^{ab}	0.39±0.02 ^b	0.41±0.01 ^b	0.38±0.02 ^{bc}	0.16±0.01 ^{ab}	0.05±0.01 ^c	0.14±0.01 ^a	32.73±1.74 ^a
F	18.82	5.21	20.12	10.03	20.14	8.52	3.33	4.58	9.64	70.81
P	0	0.001	0	0	0	0	0.01	0.002	0	0

Statistically significant differences ($p < 0.05$) indicated by different letters.

Table 2. Morphometric measurements of tilapia populations before standardized with SL along with standard deviations

Populations	Total Length (TL)	Standard Length (SL)	Dorsal Fin Length (DL)	Caudal Fin Length (CL)	Head Length (HL)	Body Width (WID)	Pectoral Fin Length (PL)	Caudal Peduncle Depth (CPD)	Eye Diameter (ED)	Snout Length (SNL)	Body Weight (BW)
Female <i>Salina</i>	24.81±1.22	20.35±1.04	12.1±0.65	4.64±0.29	7.94±0.46	8.24±0.49	6.42±0.93	3.10±0.14	1.22±0.08	2.35±0.13	333.43±47.74
Male <i>Salina</i>	27.49±1.39	22.03±1.26	13.4±0.95	5.75±0.31	9.09±0.43	9.63±0.58	7.91±0.61	3.54±0.20	1.31±0.12	2.75±0.29	450.95±66.51
Female <i>Sultana</i>	33.38±2.26	26.57±1.86	15.9±0.97	6.97±0.39	10.34±0.79	10.74±0.74	10.3±0.9	4.09±0.28	1.47±0.22	3.22±0.34	754.46±131.92
Male <i>Sultana</i>	30.03±0.94	23.7±0.74	14.28±0.45	6.61±0.44	9.8±0.31	10.28±0.42	9.08±0.67	3.79±0.18	1.52±0.15	3.09±0.20	579.52±61.12
Female <i>Red NIFI</i>	28.16±2.32	22.53±1.91	13.1±1.29	5.89±0.55	8.6±0.67	8.71±0.73	7.89±0.7	3.44±0.30	1.33±0.11	2.74±0.31	434.61±99.31
Male <i>Red NIFI</i>	37.36±1.32	29.43±0.89	17.57±0.51	7.88±0.57	11.42±0.56	11.94±0.45	9.67±0.74	4.62±0.33	1.53±0.18	3.98±0.31	964.05±72.27
Average	30.2±4.45	24.1±3.33	14.4±2.03	6.29±1.11	9.53±1.27	9.92±1.37	8.54±1.49	3.76±0.55	1.40±0.19	3.02±0.58	586.17±231.03

Table 3. Summary of effect sizes of 3 Tilapia's strain and sex parameters on standardized traits based on ANOVA p -values and partial η^2 (interpreted using Cohen's benchmarks)

Effect	Traits	p -value	η_p^2
strain	BW:SL	2.22E-16	0.737
strain:sex	BW:SL	6.92E-16	0.726
sex	BW:SL	2.44E-10	0.527
sex	WID:SL	4.59E-10	0.516
strain	TL:SL	3.78E-09	0.512
strain	CL:SL	1.18E-08	0.491
strain	WID:SL	2.95E-07	0.427
sex	CL:SL	1.8E-07	0.399
sex	SNL:SL	3.85E-07	0.382
sex	TL:SL	5.18E-07	0.375
strain	PL:SL	6.72E-06	0.357
sex	HL:SL	5.44E-06	0.320
strain	HL:SL	0.000297	0.260
strain:sex	ED:SL	0.000738	0.234
sex	CPD:SL	0.00039	0.210
strain	SNL:SL	0.002576	0.198
strain:sex	CL:SL	0.003434	0.190
strain:sex	PL:SL	0.004006	0.185
strain	DL:SL	0.004783	0.180
sex	DL:SL	0.001323	0.175
strain	ED:SL	0.050172	0.105
strain:sex	HL:SL	0.065534	0.096
strain:sex	TL:SL	0.096441	0.083
strain:sex	WID:SL	0.242386	0.051
strain:sex	DL:SL	0.258895	0.049
strain:sex	SNL:SL	0.484492	0.026
strain	CPD:SL	0.54491	0.022
strain:sex	CPD:SL	0.577618	0.020
sex	PL:SL	0.522109	0.008
sex	ED:SL	0.916752	0.000

Statistical significance expressed by $p < 0.05$, while stronger effect on traits expressed by higher η_p^2 .

Table 4. PCA summary on 10 standardized morphometric traits of 60 samples within 6 populations

	PC1	PC2
% Variance	38.17%	22.62%
Standard deviation	1.9537	1.5039
Variable	Loadings	
TL:SL	-0.3900894	-0.3330611
DL:SL	-0.1774408	0.24706297
CL:SL	-0.4086349	-0.2381186
HL:SL	-0.3609769	0.39050834
WID:SL	-0.3629046	0.36461521
PL:SL	-0.2701067	0.02182457
CPD:SL	-0.3973716	0.17385839

ED:SL	-0.05006277	0.44217524
SNL:SL	-0.3061702	-0.2589871
BW:SL	-0.2454592	-0.4388535

The dimension axis of PC1 explains the most variance, following the dimension PC2. Higher loading value indicates that the variable has a stronger contribution to the principal component.

Table 5. Length-Weight model performance comparison for standard (Le Cren) and piecewise regression approaches across 6 tilapia populations

Population	Model	RMSE	Max Abs Bias	AIC*
Female <i>Salina</i>	Le Cren	22.38	14.11	-18.86
	Piecewise	21.57	11.98	-15.88
Male <i>Salina</i>	Le Cren	9.44	5.40	-42.14
	Piecewise	8.93	4.12	-39.58
Male <i>Red NIFI</i>	Le Cren	41.28	10.54	-29.42
	Piecewise	10.47	2.42	-51.66
Female <i>Red NIFI</i>	Le Cren	28.57	10.98	-21.39
	Piecewise	13.09	6.76	-29.06
Male <i>Sultana</i>	Le Cren	34.86	9.26	-22.81
	Piecewise	17.67	5.99	-30.91
Female <i>Sultana</i>	Le Cren	36.73	9.32	-27.84
	Piecewise	34.83	9.95	-24.75

*indicates that for model selection, the lower the value means better fit model.

Values for RMSE (root mean square error) and Max Abs Bias are in grams. AIC is Akaike's Information Criterion.

Table 6. Length-weight relationship of each tilapia population calculated using the standard model (Le Cren, 1951)

Population	n	Standard Length (SL)	Body Weight (BW)	<i>a</i>	<i>b</i>
Female <i>Salina</i>	10	20.35±1.04	333.43±47.74	-0.7373	2.4895
Male <i>Salina</i>	10	22.03±1.26	450.95±66.51	-0.8496	2.6068
Female <i>Sultana</i>	10	26.57±1.86	754.46±131.92	-0.8222	2.5945
Male <i>Sultana</i>	10	23.70±0.74	579.52±61.12	-1.1973	2.8795
Female <i>Red NIFI</i>	10	22.53±1.91	434.61±99.31	-0.4729	2.2958
Male <i>Red NIFI</i>	10	29.43±0.89	964.05±72.27	0.0385	2.0050

If the *b* value = 3.00, this indicates isometric growth, *b* < 3.00 indicates a negative allometric growth, *b* value > 3.00 suggests a positive allometric growth.

playing key roles, while external environmental factors, including water quality, temperature, and food availability. Consequently, K measurements offer valuable data for assessing habitat quality and guiding fishery management efforts to sustain population health (Adeogun *et al.*, 2016; Reyes, 2024). Moreover, post hoc analysis confirmed

that male and female *Salina* strains had significantly higher condition factors than their *Red NIFI* counterparts, indicating that genetic strain plays a role in growth performance. These results are consistent with findings from Gunadi *et al.* (2021), who reported variability in K values among tilapia strains in Indonesia. Furthermore,

environmental factors such as sex and geographical location have been identified as significant factors to variations in K values, reinforcing the complexity of growth performance evaluation in aquaculture systems (Oyebola *et al.*, 2022). In aquaculture context, the condition factor is a crucial parameter that reflects the physiological and nutritional status of fish. A higher K value generally indicates better growth performance and exhibits better feed conversion ratios (FCR) (Barylo *et al.*, 2021).

The length-weight relationship (LWR) in fish biology is a crucial parameter for understanding growth dynamics by correlating length and weight (Jisr *et al.*, 2018). In this study, we compared the performance of 2 known models: standard Le Cren and Piecewise regression for LWR analysis of 6 tilapia populations as shown in Table 5. The Piecewise regression model occasionally yielded slightly lower Root Mean Square Error (RMSE) and bias values than the standard allometric model (Le Cren), particularly in male *Red NIFI* and female *Red NIFI*. However, these improvements were not consistent across all populations, and the associated AIC differences were modest in several cases (e.g., female *Salina* and female *Sultana*). Applying the standard Le Cren model uniformly offers important advantages: it maintains a simple, biologically interpretable form through a single exponent (b) that captures the length-weight scaling, facilitates direct comparison among populations, and avoids the risk of overfitting to population-specific irregularities that may reflect sampling variation rather than true biological shifts. As for interpretation, the b value of the LWR equal to 3 indicates isometric growth, where weight and length increase proportionally. The b value less than 3 indicates negative allometric growth, meaning weight increases more slowly than length, which is typical of organisms that become slimmer as they grow. Conversely, the b value greater than 3 suggests positive allometric growth, where weight increases more rapidly than length (Asmamaw *et al.*, 2019; Jisr *et al.*, 2018). Given its broad acceptance in fisheries science as a benchmark for length-weight analysis, the

standard Le Cren model provides a coherent and comparable framework for interpreting growth patterns across diverse populations in this study.

We found that all the populations have a b value lower than 3 indicating all the populations have negative allometric growth (Table 6 and Figure 7). The male *Sultana* groups have a b value closest to 3 (2.8795), indicating more proportional length and weight compared to other populations. The lowest b value was found in male *Red NIFI* (2.005), suggesting this strain possesses the slimmest body type among the groups. Both male and female *Salina* have b values greater than both male and female *Red NIFI*, meaning the *Salina* strain has a more proportional body compared to the *Red NIFI* strain. This suggests that *Salina* has a genetic adaptation that favours their balanced development, including greater adaptability to both freshwater and brackish water environments, which allows efficient energy utilization and steady growth, unlike the *Red NIFI* strain, which may exhibit less balanced development in terms of the length-weight growth. Environmental factors, including water quality and feeding inputs, can also influence growth patterns, contributing to the observed differences in LWR across strains. Variations in parameters such as dissolved oxygen, temperature, pH, and nutrient availability directly affect metabolic efficiency, feed utilization, and overall physiological performance. Likewise, differences in feed quality, nutrient composition, and feeding regimes can alter growth trajectories by influencing protein synthesis, lipid deposition, and energy allocation. These environmental interactions not only shape condition factors and morphometric traits but may also interact with genetic backgrounds, amplifying or masking inherent strain-specific growth potential (Kamble *et al.*, 2024; Washim *et al.*, 2022). In this study, we obtained the b values of the Length-Weight Relationship (LWR) ranging from 2.0050 to 2.8795, is consistent with the findings of previous reports indicating that b values for tilapia was between 2 and 4 (Diallo *et al.*, 2022; Kamble *et al.*, 2024; Wagaw *et al.*, 2024). The negative allometry observed in this study indicates that

body weight increases at a slower rate than body length. This pattern suggests a growth strategy in which energy is preferentially allocated to linear growth rather than mass accumulation, which may confer advantages such as improved swimming efficiency and reduced predation risk during early life stages (Xie *et al.*, 2024). From a physiological perspective, negative allometry may reflect metabolic scaling, where lower maintenance energy requirements allow more resources to be directed toward reproductive output and survival under challenging environmental conditions. This pattern suggests that individuals with relatively smaller body sizes may possess adaptive advantages in environments with limited resources, as their reduced energetic demands enable greater allocation of nutrients and energy to essential functions such as gametogenesis, immune defense, and stress resilience. Consequently, negative allometry can be interpreted not only as a constraint of growth but also as an adaptive strategy that optimizes fitness and enhances long-term population persistence in fluctuating or resource-poor habitats (Wiff and Roa-Ureta, 2008; Pontzer and McGrosky, 2022).

The coefficient of determination, or R-squared (R^2), is a key metric in regression analysis that quantifies the proportion of variance in the dependent variable explained by the model's independent variables. It reflects the model's explanatory power, with values ranging from 0 to 1, where higher values denote a better fit of the model to the observed data (Chicco *et al.*, 2021). In this study, the R^2 values for the length-weight relationship (LWR) ranged from 0.6602 to 0.9776. An R^2 value above 0.9 indicates a strong correlation between weight and length, demonstrating that length is highly accurate predictor of weight (Deekrachang *et al.*, 2024). Specifically, R^2 value above 0.9 were observed in male *Salina* and female *Sultana* strains, suggesting particularly robust LWR. A slightly lower R^2 value of 0.8957 was found in female *Red NIFI* group, while female *Salina* group exhibited an R^2 value of 0.7526. Male *Sultana* and male *Red NIFI* had R^2 values below 0.7, indicating a weaker correlation between length and weight in these

groups. In biological research, an R^2 values above 0.7 are generally considered strong, values between 0.3 and 0.7 reflect a moderate correlation, and values below 0.3 reflect a weak correlation (Rusakov, 2023). These findings highlight the variability in LWR among different strains, which may be influenced by genetic factors, environmental conditions or strain-specific growth patterns.

CONCLUSION

The results revealed overlapping morphometric traits across most populations, with the exception of female *Salina*, which exhibited slight but distinct differences likely reflecting unique traits acquired from crossbreeding between two different strains. Male *Salina*, in contrast, showed morphometric traits closely aligned with its male parent, the *Sultana* strain. The condition factor across all populations indicated favourable growth conditions; however, the observed negative allometric growth pattern suggests that length increases more rapidly than body weight, potentially reflecting adaptive trade-offs in suboptimal environments. While these findings provide important phenotypic insights relevant to breeding strategies, several limitations must be acknowledged. Each strain was reared in a separate pond, with males and females housed in hapas within the same pond. As such, strain and pond effects were confounded, preventing complete separation of genetic influences from environmental effects. Although pond was accounted for as a blocking factor in the statistical analysis, the absence of pond replication means that subtle environmental influences cannot be entirely excluded. Given its low cost, minimal equipment requirements, and proven reliability, the morphometric baseline established in the present study can serve as a practical reference for future applications, including strain certification, selective breeding programs targeting desirable growth and body shape traits, and ecological adaptation assessments to optimize aquaculture performance across different environments. Overall, this research provides the first morphological evidence on the hybridization

outcomes of *Salina* tilapia under suboptimal salinity, offering insight into their growth patterns, potential reproductive trade-offs, and the balance between hybrid vigor and parental resemblance. The findings also underscore the economic relevance of selective breeding strategies that enhance salinity resilience in tilapia. In hatchery operations, incorporating broodstock that demonstrate tolerance to suboptimal salinity conditions can improve fry survival, growth performance, and overall production stability. For farmers, the use of hybrids such as the *Salina* strain, particularly when reared in environments closer to their optimal salinity range which may reduce mortality, shorten grow-out periods, and lower feed conversion ratios, ultimately increasing profitability. Future research directions should incorporate replicated common-garden designs to better isolate genetic effects and strengthen evidence for potential maternal dominance effects observed in the *Salina* strain. In addition, integrating molecular approaches such as microsatellite analysis, mitochondrial DNA sequencing, and SNP genotyping will be essential to complement morphological data and more robustly characterize the genetic diversity and population structure of these tilapia strains.

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AUTHORS' CONTRIBUTIONS

YPB conceived and designed the study. KMD was responsible for fieldwork, fish sampling, and morphometric measurements. Data entry, validation, and statistical analyses were conducted by EIR, HW, WS, and RSA. SS, AFL,

MKF, and NM assisted with the literature review and data interpretation. AA, ARA, IC, and DY contributed to manuscript writing, formatting, and final editing. All authors have read, reviewed, and approved the final version of the manuscript.

COMPETING INTERESTS

The authors declare that they have no competing interests.

REFERENCES

- Adeogun, A. O., Ibor, O. R., Regoli, F., & Arukwe, A. (2016). Peroxisome proliferator-activated receptors and biotransformation responses in relation to condition factor and contaminant burden in tilapia species from Ogun River, Nigeria. *Comparative Biochemistry and Physiology Part - C: Toxicology and Pharmacology*, 183–184, 7–19.
- Albani, R. I., Budiardi, T., Hadiroseyani, Y., & Ekasari, J. (2023). Production performance of Nile tilapia *Oreochromis niloticus* and mineral balance in aquaponic, biofloc, and aquabioponic culture systems. *Jurnal Akuakultur Indonesia*, 22(1), 66–79.
- Aliah, R. S. (2017). Rekayasa Produksi Ikan Nila Salin Untuk Perairan Payau di Wilayah Pesisir. *Jurnal Rekayasa Lingkungan*, 10(1), 17–24.
- Allaman, I. B., Neto, R. V. R., de Freitas, R. T. F., Freato, T. A., Lago, A. de A., Costa, A. C., & de Lima, R. R. (2013). Weight and morphometric growth of different strains of tilapia (*Oreochromis* sp). *Revista Brasileira de Zootecnia*, 42(5), 305–311.
- Ariyanto, D. (2002). Analysis Of Body Shape Variability Of Nile Tilapia Strain Gift In Three Different Levels Of Age. *Gadjah Mada University Journal Fish Science*, IV (1), 19–26.
- Asmamaw, B., Tessema, M., Beyene, B., & Assefa, A. (2019). Length-weight relationships and condition factor of Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758) (Cichlidae) in Koka Reservoir,

- Ethiopia. *International Journal of Fisheries and Aquatic Research*, 4(3), 331438089.
- Barylo, Ye., Loboiko, Yu., Barylo, B., Keznine, M., & Benaissa, H. (2021). Condition factor and identification of amino acid composition of three trout species in the western region of Ukraine. *Egyptian Journal of Aquatic Biology and Fisheries*, 25(4), 539–548.
- Chicco, D., Warrens, M. J., & Jurman, G. (2021). The coefficient of determination R-squared is more informative than SMAPE, MAE, MAPE, MSE and RMSE in regression analysis evaluation. *PeerJ Computer Science*, 7, 1–24.
- De Robertis, A., & Williams, K. (2008). Weight-Length Relationships in Fisheries Studies: The Standard Allometric Model Should Be Applied with Caution. *Transactions of the American Fisheries Society*, 137(3), 707–719.
- Deekrachang, C., Grudpun, C., Suvarnaraksha, A., Phomikong, P., & Jutagate, T. (2024). Length-Weight Relationship and Condition Factor of Fishes in Two Major Rivers, the Chao Phraya and the Bang Pakong, in Thailand. *Tropical Life Sciences Research*, 35(1), 257–273.
- Dewi, K. M., Hubeis, A. V. S., & Raharja, S. (2018). Development Strategy of Salina Tilapia (*Oreochromis* sp.) Culture as New Varieties of Aquaculture. *Manajemen IKM*, 13(1), 66–74.
- Diallo, F. L., Ly, M. A., Diop, L., Diatta, I., & Seck, S. M. (2022). Growth response of Nile Tilapia (*Oreochromis niloticus*) stocked at different densities in the LAKE-Kalassane basin in northwestern Senegal. *International Journal of Biological and Chemical Sciences*, 16(5), 1919–1928.
- Diego, T. J. A. S., Al-Shaer, M. A. Q., & Jamali, E. A. H. Al. (2023). Re-evaluating eurahaline nature of Nile tilapia, *Oreochromis niloticus*: A hatchery perspective. *International Journal of Fisheries and Aquatic Studies*, 11(5), 223–231.
- Engdaw, F. (2023). Morphometric relations and diet compositions of Nile tilapia *Oreochromis niloticus* (Linn. 1758) in Lake Tana Gorgora gulf, Ethiopia. *Fisheries and Aquatic Sciences*, 26(3), 169–180.
- Faqih, I. S., Soelistyowati, D. T., & Carman, O. (2015). Phenotypes performance of tilapia best, nirwana II, jatimbulan, and sultana using floating net, and pond culture system. *Jurnal Iktiologi Indonesia*, 15(3), 193–200.
- Gunadi, B., Setyawan, P., & Robisalmi, A. (2021). Growth, length-weight relationship, and condition factor of NIFI (*Oreochromis* sp.) and Srikandi Tilapia (*Oreochromis aureus* x *niloticus*) at the grow-out stage in the high salinity brackishwater ponds. *Jurnal Iktiologi Indonesia*, 21(2), 117–130.
- Gustiano, R., Arifin, O. Z., Subagja, J., Kurniawan, K., Prihadi, T. H., Saputra, A., Ath-Thar, M. H. F., Cahyanti, W., Prakoso, V. A., Radona, D., Kusmini, I. I., & Kristanto, A. H. (2023). The Success of Freshwater Aquaculture Program: Nile Tilapia or Nila Culture in Indonesia. *Zuriat*, 34(2), 56.
- Hasan, M., Hosen, M. H. A., Miah, M. I., Ahmed, Z. F., Chhanda, M. S., & Shahriar, S. I. M. (2020). Fecundity, length at maturity and gonadal development indices of river catfish (*Clupisoma garua*) of the old Brahmaputra River in Bangladesh. *The Egyptian Journal of Aquatic Research*, 46(3), 259–263.
- Htun-Han, M. (1978). The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: gonosomatic index, hepatosomatic index and condition factor. *Journal of Fish Biology*, 13(1), 32.
- Jisir, N., Younes, G., Sukhn, C., & El-Dakdouki, M. H. (2018). Length-weight relationships and relative condition factor of fish inhabiting the marine area of the Eastern Mediterranean city, Tripoli-Lebanon. *Egyptian Journal of Aquatic Research*, 44(4), 299–305.
- Jonsson, N., & Jonsson, B. (1999). Trade-off between egg mass and egg number in brown trout. *Journal of Fish Biology*, 55(4), 767–783.
- Joshi, R., Meuwissen, T. H. E., Woolliams, J. A., & GjØen, H. M. (2020). Genomic dissection

- of maternal, additive and non-additive genetic effects for growth and carcass traits in Nile tilapia. *Genetics Selection Evolution*, 52(1), 67.
- Kamble, M. T., Salin, K. R., Chavan, B. R., Medhe, S. V., Thompson, K. D., & Pirarat, N. (2024). Length-weight relationship and condition factor of Nile tilapia (*Oreochromis niloticus*) fed diets supplemented with guava and star gooseberry leaf extract. *F1000Research*, 13, 540.
- Koenigbauer, S. T., & Höök, T. O. (2023). Increased offspring provisioning by large female fish and consequences for reproductive efficiency. *Ecology and Evolution*, 13(10), 99.
- Kosai, P., Sathavorasmitth, P., Jiraungkoorskul, K., & Jiraungkoorskul, W. (2014). Morphometric Characters of Nile Tilapia (*Oreochromis niloticus*) in Thailand. *Agriculture Technology and Biological Sciences Walailak*, 11(10), 130.
- Kurniawan, A., Siegers, W. H., Akbar, M. A., & Nur, I. S. M. (2023). The Production Model of Tilapia (*Oreochromis niloticus*) Cultivation with System Dynamics Approach. *Journal of Aquaculture and Fish Health*, 12(1), 21–30.
- Kwikiriza, G., Yegon, M. J., Byamugisha, N., Beingana, A., Atukwatse, F., Barekye, A., Nattabi, J. K., & Meimberg, H. (2023). Morphometric Variations of Nile Tilapia (*Oreochromis niloticus*) (Linnaeus, 1758) Local Strains Collected from Different Fish Farms in South Western Highland Agro-Ecological Zone (SWHAEZ), Uganda: Screening Strains for Aquaculture. *Fishes*, 8(4), 64.
- Laskar, B. A., Bhattacharjee, M. J., Dhar, B., Mahadani, P., Kundu, S., & Ghosh, S. K. (2013). The Species Dilemma of Northeast Indian Mahseer (Actinopterygii: Cyprinidae): DNA Barcoding in Clarifying the Riddle. *PLoS ONE*, 8(1), 91.
- Le Cren, E. D. (1951). The Length-Weight Relationship And Seasonal Cycle In Gonad Weight And Condition In The Perch (*Perca fluviatilis*). *Journal of Animal Ecology*, 20(2), 65.
- Le Moan, A., Bekkevold, D., & Hemmer-Hansen, J. (2021). Evolution at two time frames: ancient structural variants involved in post-glacial divergence of the European plaice (*Pleuronectes platessa*). *Heredity*, 126(4), 668–683.
- MMAF [Ministry of Marine Affairs and Fisheries]. (2024). Analysis of Key Performance Indicators in the Marine and Fisheries Sector for the Period 2019–2023 Vol. 2.
- Munguti, J. M., Nairuti, R., Iteba, J. O., Obiero, K. O., Kyule, D., Opiyo, M. A., Abwao, J., Kiriimi, J. G., Outa, N., Muthoka, M., Githukia, C. M., & Ogello, E. O. (2022). Nile tilapia (*Oreochromis niloticus* Linnaeus, 1758) culture in Kenya: Emerging production technologies and socio-economic impacts on local livelihoods. *Aquaculture, Fish and Fisheries*, 2(4), 265–276.
- Ndiwa, T. C., Nyingi, D. W., Claude, J., & Agnèse, J. F. (2016). Morphological variations of wild populations of Nile tilapia (*Oreochromis niloticus*) living in extreme environmental conditions in the Kenyan Rift-Valley. *Environmental Biology of Fishes*, 99(5), 473–485.
- Nugroho, K. C., Rizky, P. N., Harijono, T., Halim, A. M., Nasuki, & Ritonga, L. B. R. (2024). Comparative Study of Growth Performance of Three Tilapia Strain in Intensive Culture System. *IOP Conference Series: Earth and Environmental Science*, 1328(1), 652.
- Nurchayati, S., Haeruddin, Basuki, F., & Sarjito. (2021). Analysis on Land Suitability Cultivation of Saline Tilapia (*Oreochromis niloticus*) at The Pond in Tayu District. *Indonesian Journal of Fisheries Science and Technology Available*, 17, 224.
- Ondang, H. M. P., Saranga, R., & Tumanduk, N. M. (2019). Constituent genetic characteristics of scad species (family Carangidae) from Bitung waters of Indonesia. *Russian Journal of Agricultural*

- and *Socio-Economic Sciences*, 91(7), 383–390.
- Oyebola, O. O., Omitoyin, S. B., Hounhoedo, A. O. O., & Agadjihouédé, H. (2022). Length-weight relationship and condition factor revealed possibility of mix strains in *Clarias gariepinus* population of Oueme Valley, Benin Republic (West Africa). *Total Environment Research Themes*, 3–4.
- Pontzer, H., & McGrosky, A. (2022). Balancing growth, reproduction, maintenance, and activity in evolved energy economies. *Current Biology*, 32(12), R709–R719.
- Ramli, M. Z. (2016). Characterization of Four Red Hybrids Tilapia (*Oreochromis* sp.) through Morphometric Characteristics. *Academia Journal of Agricultural Research*, 4(6), 382–386.
- Rasheeq, A. A., Rajesh, M., Kumar, T. T. A., Rajesh, K. M., Kathirvelpandian, A., Kumar, S., & Singh, P. K. (2023). Stock structure analysis of the white-spotted spine foot fish (*Siganus canaliculatus*) along the Indian coast using Truss morphometry. *Regional Studies in Marine Science*, 65(1), 71.
- Regala, J. A., Fernando, S. I. D., & Velasco, R. R. (2018). Morphometric Differentiation Among Four Populations of Red Tilapia (*Oreochromis* spp.). *International Journal of Biology, Pharmacy and Allied Sciences*, 7(6), 99.
- Reyes, A. T. (2024). Comparison of Fulton's Condition Factor of Nile Tilapia (*Oreochromis niloticus* L.) Reared in Ponds in Lubao, Pampanga, Philippines During the Dry Season. *Uttar Pradesh Journal of Zoology*, 45(15), 406–416.
- Rusakov, D. A. (2023). A misadventure of the correlation coefficient. *Trends in Neurosciences*, 46(2), 94–96.
- Setyawan, P., Aththar, M. H. F., Imron, I., Gunadi, B., Haryadi, J., Bastiaansen, J. W. M., Camara, M. D., & Komen, H. (2022). Genetic parameters and genotype by environment interaction in a unique Indonesian hybrid tilapia strain selected for production in brackish water pond culture. *Aquaculture*, 561(2), 112.
- Shuai, F., & Li, J. (2022). Nile Tilapia (*Oreochromis niloticus* Linnaeus, 1758) Invasion Caused Trophic Structure Disruptions of Fish Communities in the South China River—Pearl River. *Biology*, 11(11), 94.
- Silva, A. (2003). Morphometric variation among sardine (*Sardina pilchardus*) populations from the northeastern Atlantic and the western Mediterranean. *ICES Journal of Marine Science*, 60, 1352–1360.
- Taukhid, T., Lusiastuti, A. M., Novita, H., Caruso, D., Avarre, J. C., Sugiani, D., Kholidin, E. B., Saputra, A., Widyastuti, Y. R., & Andriyanto, S. (2024). Resistance of Indonesian tilapia strains, *Oreochromis niloticus* to Tilapia Lake Virus Disease (TiLVD). *Bulletin of the European Association of Fish Pathologists*, 44(1), 81.
- Tripathy, S. K. (2020). Significance of Traditional and Advanced Morphometry to Fishery Science. *Journal of Human, Earth, and Future*, 1(3), 153–166.
- Quémeneur, J., Danion, M., Cabon, J., Collet, S., Zambonino-Infante, J., & Salin, K. (2022). The relationships between growth rate and mitochondrial metabolism varies over time. *Scientific Reports*, 12(1), 154.
- Wagaw, S., Sisay, A., Bazezew, A., Enawgaw, Y., & Wosnie, A. (2024). Biological aspects of *Oreochromis niloticus* (Linnaeus, 1758) in Geray Reservoir (Ethiopia) for effective sustainable fisheries. *Fisheries and Aquatic Sciences*, 27(2), 100–110.
- Wahidah, Rusli, A., Hartinah, Amrullah, & Dwinhoven, I. (2023). Evaluation of body performance of tilapia (*Oreochromis niloticus*). *IOP Conference Series: Earth and Environmental Science*, 1273(1), 89.
- Washim, Md. M. R., Rubel, A. K. M. S. A., Mondal, D. K., Ahmmed, S., Sakib, Md. H., Rahman, S. L., & Islam, Md. L. (2022). Evaluation of growth performance of three strains of Nile tilapia *Oreochromis niloticus* (L., 1758) and relation with water physico-chemical parameters reared in brackishwater ponds, Bangladesh. *Journal of Aquaculture and Fish Health*, 11(2), 170–181.

- Wiff, R., & Roa-Ureta, R. (2008). Predicting the slope of the allometric scaling of consumption rates in fish using the physiology of growth. *Marine and Freshwater Research*, 59(10), 912.
- Xie, M., Wang, P., Deng, Q., Liu, S., Zhang, Z., Wu, H., Xiang, J., Zhou, J., Yang, X., Song, R., Li, S., & Xie, Z. (2024). Allometric Growth Pattern and Hunger Tolerance of *Hemibarbus maculatus* Bleeker Larvae. *Biology*, 13(3), 164.
- Yu, C. C., Quinn, J. T., Dufournaud, C. M., Harrington, J. J., Rogers, P. P., & Lohani, B. N. (1998). Effective dimensionality of environmental indicators: a principal component analysis with bootstrap confidence intervals. *Journal of Environmental Management*, 53(2), 135.
- Zhang, T., Yang, Y., Liu, Y., Liu, C., Zhao, R., Li, D., & Shi, C. (2024). Fully automatic system for fish biomass estimation based on deep neural network. *Ecological Informatics*, 79, 102399.
